植物研究雑誌
J. Jpn. Bot.
80: 125–160 (2005)

Originals

Pollen Morphology of the Japanese Phaseoleae (Leguminosae: Papilionoideae)

Hiroyoshi OHASHI[a], Tomoyuki NEMOTO[b] and Ryuichi ONODERA[c]

Biological Institute, Faculty of Science, Tohoku University, Sendai, 980-8578 JAPAN
[a]Present address: Botanical Garden, Tohoku University, Sendai, 980-0862 JAPAN
E-mail: ohashi@mail.tains.tohoku.ac.jp
[b]Present address: Department of Basic Sciences, Ishinomaki Senshu University,
Ishinomaki, Miyagi, 986-8580 JAPAN
[c]Present address: [redacted] Katsushika-ku, Tokyo, 124-[redacted] JAPAN

(Received on November 6, 2004)

Pollen grains of all the species in the tribe Phaseoleae (Leguminosae: Papilionoideae) native to Japan (13 gen. 30 spp.) and one introduced species (*Erythrina variegata* L.) were described and illustrated on the basis of observation with scanning electron and light microscopes. Keys to the genera and species based on the pollen morphology are provided. Taxonomic problems within *Amphicarpaea* and *Vigna* are discussed.

Key words: *Amphicarpaea*, Japan, Leguminosae, Phaseoleae, pollen morphology.

Phaseoleae DC. is the largest and most polymorphic tribe in the subfamily Papilionoideae of Leguminosae. It comprises 10 subtribes covering 89 genera with a total of ca. 1500 species (Lackey 1977), or 83 genera (Polhill 1994). The pollen morphology of the tribe has been studied extensively compared with the rest of the subfamily (cf. Erdtman 1966, 1969, Makino 1978, Ferguson and Skvarla 1981, Ferguson 1984 and many studies in *Butea*, *Erythrina*, *Mucuna*, tribe Diocleinae, etc.). Results of such studies have demonstrated the significance of pollen morphology in the taxonomy of the tribe. Remarkable examples include generic delimitation in the *Dolichos* complex (Bronkers and De Keyser 1966, Verdcourt 1970a) and the *Phaseolus-Vigna* complex (Verdcourt 1970b, Stainier 1974, 1976, Stainier and Horvat 1978, Maréchal et al. 1978, Horvat and Stainier 1980). The distinctive pollen of *Kerstinguiella* of the tribe Desmodieae examined by Ohashi (1971) resulted in the genus being treated as congeneric with *Macrotyloma* of Phaseoleae (Maréchal and Baudet 1977, Verdcourt 1978). Also, a monotypic genus, *Voandzeia* of the Phaseoleae, a widely cultivated geocarpic plant for crop in tropics, was transferred into *Vigna* of the same tribe based in part on their similarity in pollen exine pattern (Maréchal et al. 1978, Verdcourt 1978, 1980). The pollen features indicate close relationships between the genera or species in Phaseoleae, but Ferguson and Skvarla (1981) pointed out that the pollen features hardly reflect the macromorphology characterizing the subtribes of Phaseoleae as proposed by Lackey (1977, 1981). Recent phytochemical and molecular systematic analyses suggest polyphyly of the Phaseoleae (Viviani et al. 1991, Bruneau et al. 1995, Doyle et al. 2000, Kajita et al. 2001, Wojciechowski 2003). Further extensive surveys on pollen morphology as well as other morphological taxonomic characters are needed for a better taxonomic system of the tribe Phaseoleae.

The native Japanese Phaseoleae comprise 30 species in 13 genera (Ohashi 1999, 2001). It is 13 % of the world genera (83 genera in Polhill 1994) and 0.02 % of the whole species (ca. 1500 in Lackey 1977). Their pollen morphologies are known only from a small number of species examined with light microscopy (LM). Ikuse (1956) examined eight species in seven genera; Shimakura (1973) four in four genera; and Nakamura (1980) eight species in seven genera. Most of the species were repeatedly observed in these works, and in fact only pollen grains of 10 species of nine genera are known for Japanese Phaseoleae. They are; one speices each of *Amphicarpaea*, *Apios*, *Canavalia*, *Dumasia*, *Dunbaria*, *Glycine*, *Pueraria*, and *Rhynchosia* and two species of *Vigna*. Pollen of *Vigna angularis* has been examined by scanning (SEM) and trasmission (TEM) electron microscopy to determine its systematic position (Ohashi and Takahasi 1981).

This paper aims to provide pollen data of the Japanese Phaseoleae in contribution to a better taxonomic system of the tribe, as well as for a pollen flora of Japanese legumes. It presents pollen morphology of thirty-one species from 14 genera including *Erythrina variegata* L. It is uncertain whether this species is naturally distributed in the Ryukyus (Nansei-shoto), and Bonin Isl. (Ogasawara-shoto) or artificially introduced for cultivation.

Materials and Methods

Pollen grains were taken from herbarium specimens in TUS, except *Glycine tabacina* (Labill.) Benth. from URO. All specimens were collected in Japan except those of the following three species: *Flemingia macrophylla* (Willd.) Merr. var. *philippinensis* (Merr. & Rolfe) H. Ohashi, *Flemingia strobilifera* (L.) W. T. Aiton and *Vigna adenantha* (G. F. Meyer) Marèchal et al. A list of the specimens used is given in Table 1. Pollen of *Vigna vexillata* var. *tsusimensis* was not examined in this study. Samples of this rare variety were not available for pollen examination in TUS.

Pollen grains were acetolysed following the standard method and dehydrated in an ethanol series (Erdtman 1960, Ye and Ohashi 2002). For SEM observation, pollen grains were air dried and coated with gold palladium, and examined with a Hitachi S-4100 scanning electron microscope in the Biological Institute, Faculty of Science, Tohoku University. The polar and equatorial lengths were measured on 30 grains in each sample. Pollen terminology is generally follows Fægri and Iversen (1989) and Punt et al. (1994). For LM observations in structure of the apertures, the acetolyzed grains were embedded in silicone oil.

Pollen data of *Amphicarpaea* used in the discussion of this paper were provided by J. Iketsu from her unpublished Master thesis of the Faculty of Science, Tohoku University (1988). Materials used in the thesis were different from those of this work but are cited in the legends of Figures 156 and 157. Methods for these observations were almost identical with this work.

Results

In the following descriptions, subtribes are ordered in accordance with the system of Polhill (1994), genera are in alphabetical order within the subtribes, and species are also in alphabetical order of the specific epithet within each genus. The order of the genera and species examined is in accordance with that shown in Table 1 except *Vigna*.

Descriptions of the pollen

(1) *Apios fortunei* Maxim. (Figs. 1–4, 125)

Pollen grains tricolporate; (27.0–)31.4 (–40.0) μm in polar axis, (27.5–)32.0(–35.0) μm in equatorial diameter; P/E = (0.81–)0.98 (–1.09), suboblate to prolate spheroidal in shape, depressed oval in equatorial view,

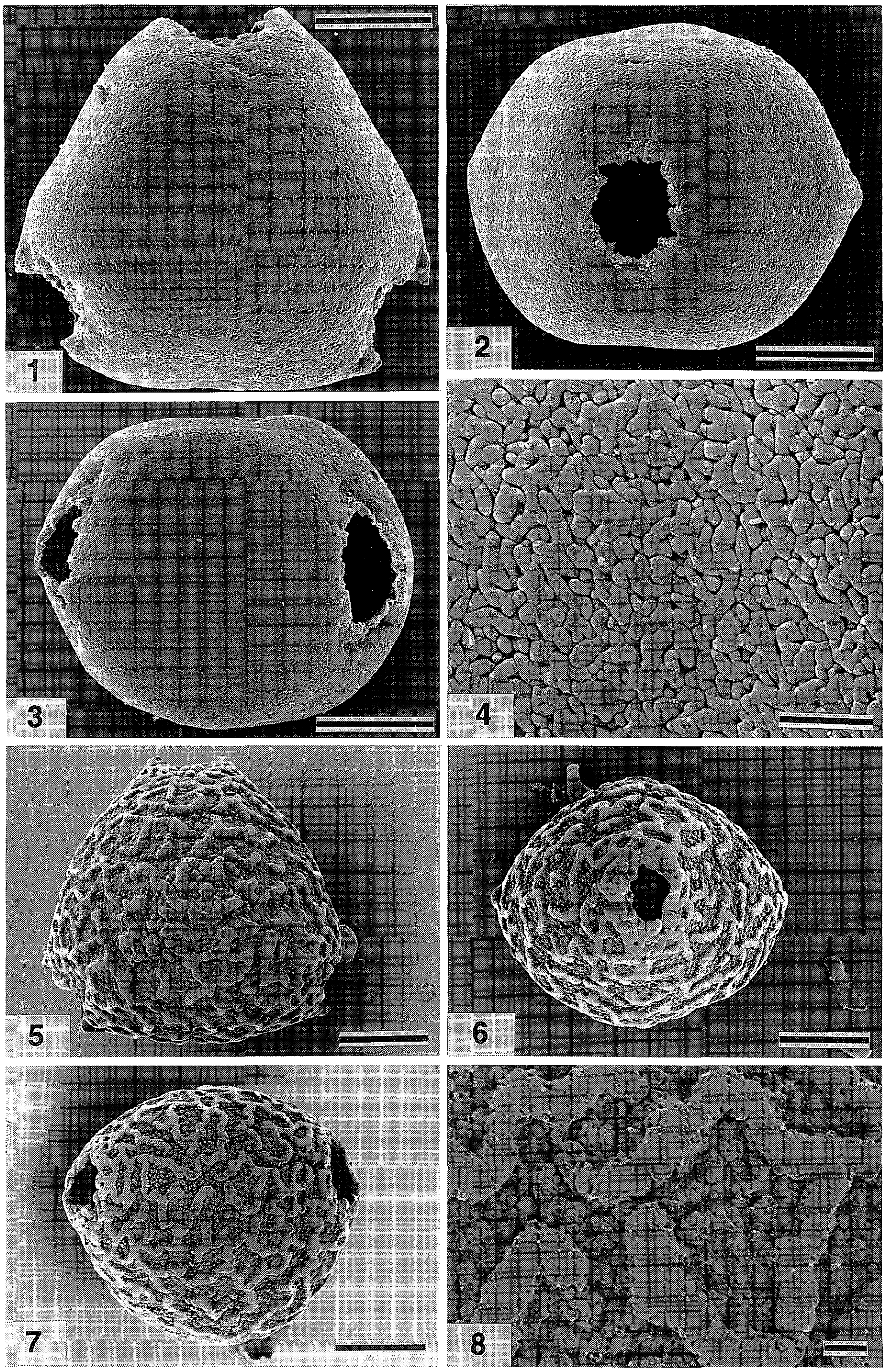
Table 1. List of specimens examined in the present study. Voucher specimens are all kept in TUS except *Glycine tabacina* kept in URO

Taxon	Voucher	Locality
Subtribe **Erythrinae**		
Apios fortunei Maxim.	G. Murata 33780	Japan, Hyogo Pref., Mt. Hunakoshi
Erythrina variegata L.	M. Furuse 2742	Japan, Okinawa Pref., Isl. Ishigaki
Mucuna gigantea (Willd.) DC.	H. Ohashi & Y. Tateishi 1277	Japan, Okinawa Pref., Isl. Ishikaki
M. macrocarpa Wall.	Y. Nishi & K. Ishizuka 147	Japan, Okinawa Pref., Isl. Okinawa
M. membranacea Hayata	Y. Tateishi 4103	Japan, Okinawa Pref., Isl. Ishigaki
M. sempervirens Hemsl.	T. Makino 80795	Japan, Kumamoto Pref.
Subtribe **Diocleinae**		
Canavalia cathartica Thouars	S. Matsumura & al. 970373	Japan, Okinawa Pref., Isl. Ishigaki
C. lineata (Thunb.) DC.	M. Takahashi 2130	Japan, Tokushima Pref., Kaifu-gun
C. rosea (Sw.) DC.	K. Shimabuku & Y. Miyagi 5629	Japan, Okinawa Pref., Isl. Iriomote
Galactia tashiroi Maxim.	Hatusima & Sako 30875	Japan, Okinawa Pref., Isl. Yoron
Subtribe **Glycininae**		
Amphicarpaea bracteata (L.) Fernald subsp. *edgeworthii* (Benth.) H. Ohashi	Y. Tateishi & H. Hoshi 11196	Japan, Saga Pref., Mt. Kurokami
Dumasia truncata Siebold et Zucc.	Y. Tateishi & al. 9633	Japan, Miyagi Pref., Tohwa-cho
Glycine koidzumii Ohwi	I. Kawakami H8923 (4)	Japan, Okinawa Pref., Isl. Miyako
G. max (L.) Merr. subsp. *soja* (Siebold et Zucc.) H. Ohashi	T. Naito & H. Ohba 71909	Japan, Miyagi Pref., Sendai-shi
G. tabacina (Labill.) Benth.	H. Ogawa 625	Japan, Okinawa Pref., Isl. Ie
Pueraria lobata (Willd.) Ohwi	J. Iketsu & H. Iketani 791	Japan, Miyagi Pref., Yamamoto-cho
P. montana (Lour.) Merr.	H. Ogawa 586	Japan, Okinawa Pref., Isl. Ie
Subtribe **Phaseolinae**		
Vigna adenantha (G. F. Meyer) Maréchal, Mascherpa & Stainier	Y. Tateishi & al. 15411	Taiwan, Isl. Lanyu
V. angularis (Willd.) Ohwi & H. Ohashi var. *nipponensis* (Ohwi) Ohwi & H. Ohashi	J. Iketsu 1342	Japan, Miyagi Pref., Kakuda-shi
V. luteola (Jacq.) Benth.	S. Matsumura 970252	Japan, Okinawa Pref., Isl. Ishigaki
V. marina (Burm.f.) Merr.	J. Murata 10361	Japan, Kagoshima Pref., Isl. Tokunoshima
V. minima (Roxb.) Ohwi & H. Ohashi		
var. *minima*	Y. Tateishi & H. Hoshi 8777	Japan, Nagasaki Pref., Isl. Uku
var. *minor* (Matsum.) Tateishi	S. Matsumura 970243	Japan, Okinawa Pref., Isl. Ishigaki
V. reflexopilosa Hayata	J. Murata 10361	Japan, Okinawa Pref., Isl. Okinawa
V. vexillata (L.) A. Rich. var. *vexillata*	Y. Takushi 11337	Japan, Okinawa Pref., Isl. Okinawa
Subtribe **Cajaninae**		
Cajanus scarabaeoides (L.) Thouars	S. Matsumura & al. 970371	Japan, Okinawa Pref., Isl. Ishigaki
Dunbaria villosa (Thunb.) Makino	J. Murata 15363	Japan, Gifu Pref., Gifu-shi
Flemingia macrophylla (Willd.) Merr. var. *philippinensis* (Merr. & Rolfe) H. Ohashi	T. Nemoto & H. Hoshi 25098	Taiwan, Hsinchu Co.
F. strobilifera (L.) R. Br.	K. Iwatsuki & al. 421	China, Yunnan, Yangbi Co.
Rhynchosia acuminatifolia Makino	K. Oka 47318	Japan, Yamaguchi Pref., Tokuyama-shi
R. minima (L.) DC.	Y. Miyagi 6626	Japan, Okinawa Pref., Isl. Hateruma
R. volubilis Lour.	H. Ohba & S. Akiyama 2420	Japan, Nagasaki Pref., Sotome-machi

subangular in polar view. Colpi ca. 0.5 times the length of polar axis, 15.8–22.5 × 3.3–8.0 μm, narrowing to rounded ends, colpus membrane granulate; endoapertures lolongate, 10.8–15 × 6.6–10.9 μm. Sexine semitectate; mesocolpium granulate to microreticulate to perforate.

(2) *Erythrina variegata* L. (Figs. 4–8, 126)

Pollen grains triporate; (27.5–)30.4(–32.5)



Figs. 1–8. SEM micrographs of pollen of *Apios fortunei* (1–4) and *Erythrina variegata* (5–8). 1, 5: Polar view. 2, 6: Equatorial view showing aperture. 3, 7: Equatorial view showing mesocolpium. 4, 8: Enlargement of mesocolpium. Scales = 10 µm (1–3, 5–7), 1 µm (4, 8).

µm in polar axis, (32.5–)33.5(–35.0) µm in equatorial diameter; P/E = (0.80–)0.91 (–1.00), suboblate to oblate spheroidal in shape, circular to rhomboidal in equatorial view, circular to semiangular in polar view. Pores lalongate to circular to lolongate, annuli with verrucae, 6.25–10.8 × 5.8–9.2 µm. Sexine semitectate; mesocolpium reticulate; muri 0.6–1.6 µm width, with puncta on margins; lumina 0.8–6.0 µm in diameter, perforate to verrucate.

(3) *Mucuna gigantea* (Willd.) DC. (Figs. 9–12, 127)

Pollen grains tricolporate; (50.0–)55.4 (–60.0) µm in polar axis, (45.0–)49.4(–57.5) µm in equatorial diameter; P/E = (1.00–)1.13 (–1.28), prolate spheroidal to subprolate in shape, circular in equatorial view, subangular to semiangular in polar view. Colpi 0.65–0.8 times the length of polar axis, 41.6–47.5 × 2–4 µm, narrowing to pointed ends, colpus membrane granulate, margins with perforate to microreticulate sculpture; endoaperture lolongate, 13.3–17.1 × 3.3–5 µm. Sexine semitectate; mesocolpium perforate, holes often with some smaller holes inside.

(4) *Mucuna macrocarpa* Wall. (Figs. 13–16, 128)

Pollen grains tricolporate; (45.0–)47.8 (–52.5) µm in polar axis, (30.0–)32.9(–37.5) µm in equatorial diameter; P/E = (1.20–)1.46 (–1.75), subprolate to prolate in shape, circular in equatorial view, circular to semiangular in polar view. Colpi ca. 0.8 times the length of polar axis, 33.3–37.5 × 2–4.2 µm, narrowing slightly to rounded ends, colpus membrane granulate, verrucate or smooth, margins with a complete tectum; endoaperture lolongate, 10.8–15 × 3.3–4.2 µm. Sexine semitectate; mesocolpium microreticulate to perforate; muri 0.5–1.3 µm wide; lumina 0.3–1 µm in diameter, more or less perforate.

(5) *Mucuna membranacea* Hayata (Figs. 17–20, 129)

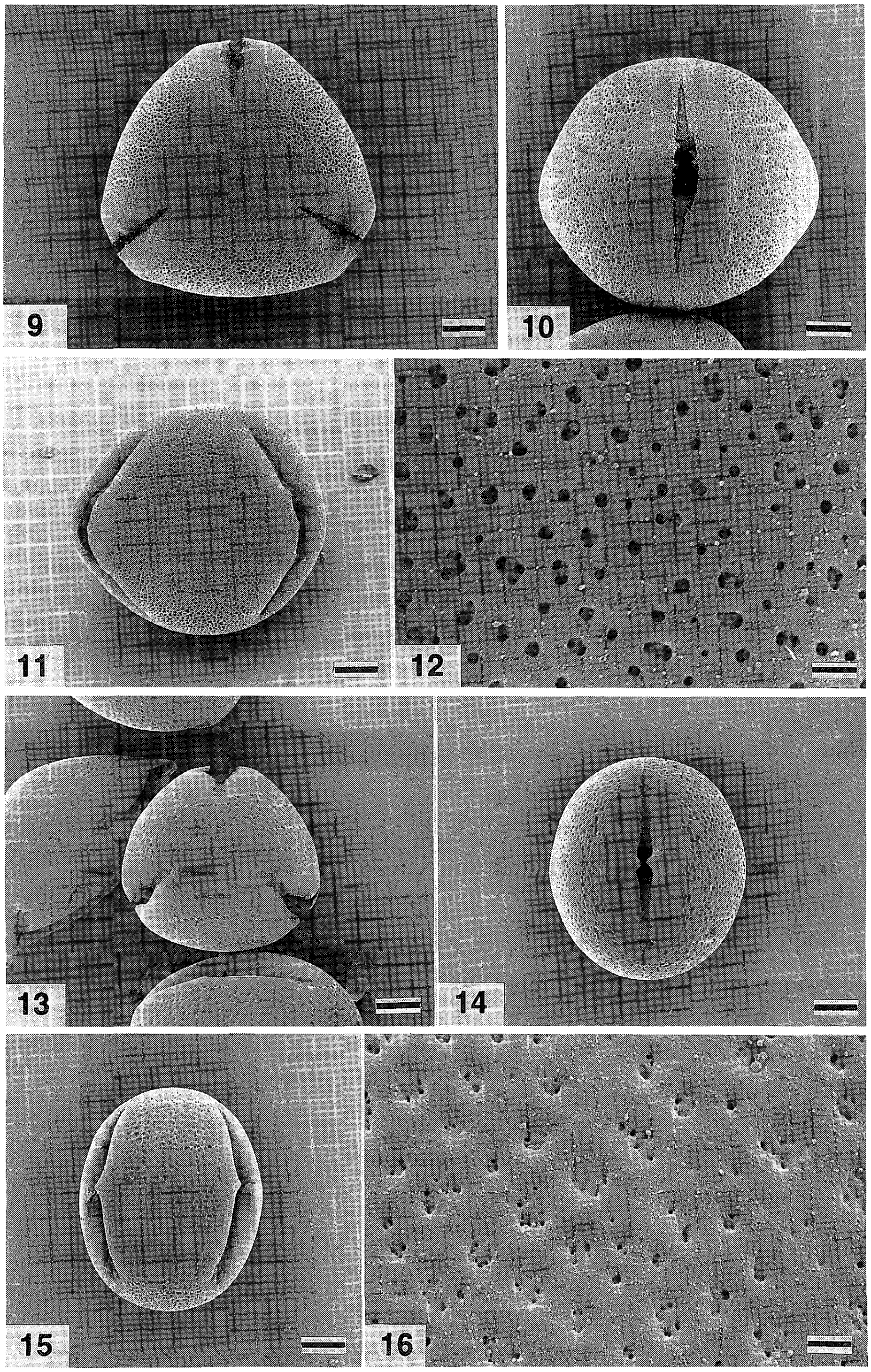
Pollen grains tricolporate; (45.0–)58.8 (–65.0) µm in polar axis, (37.5–)48.5(–57.5) µm in equatorial diameter; P/E = (1.00–)1.21 (–1.39), prolate spheroidal to prolate in shape, circular to subcircular in equatorial view and circular to semiangular in polar view. Colpi ca. 0.8 times the length of polar axis, 47.5–52.5 × 2.5–3.3 µm, narrowing to pointed ends, colpus membrane granulate to verrucate, margins with a complete tectum; endoaperture lolongate, 15–20.8 × 4.1–5 µm. Sexine semitectate; mesocolpium reticulate; muri 0.7–2.0 µm wide; lumina 1.0–3.0 µm in diameter, perforate.

(6) *Mucuna sempervirens* Hemsl. (Figs. 21–24, 130)

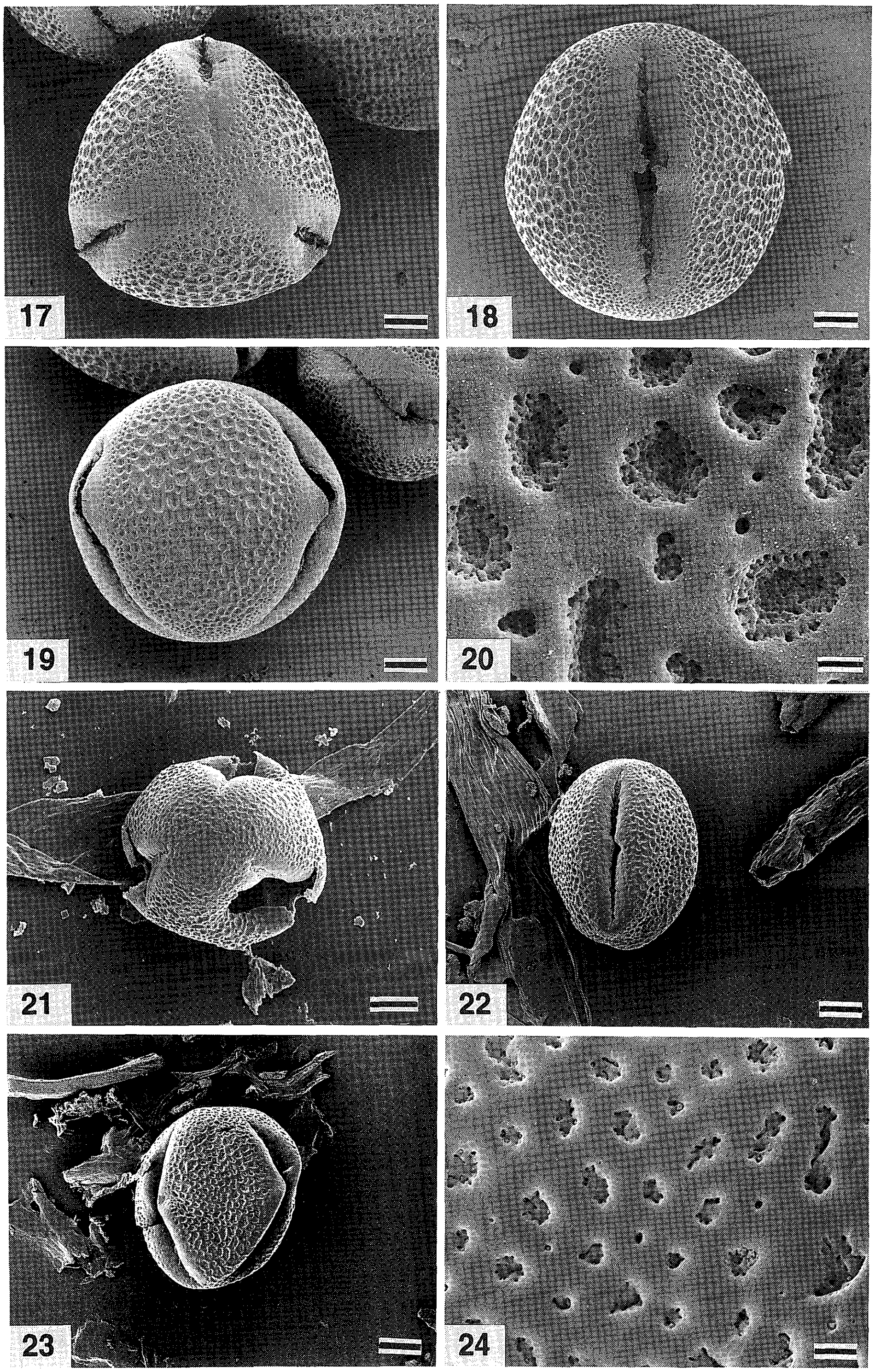
Pollen grains tricolporate; ca. 53 µm in polar axis, ca. 44 µm in equatorial diameter; P/E ≑ 1.20, subprolate in shape, subcircular in equatorial view, semiangular to circular in polar view. Colpi ca. 0.8 times the length of polar axis, ca. 3.2 × 2 µm, narrowing to pointed ends, colpus membrane with verrucae, margins with a complete tectum or microreticulate sculpture; endoaperture, lolongate, ca. 15 × 4 µm. Sexine semitectate; mesocolpium reticulate; lumina 0.8–1.8 µm in diameter.

(7) *Canavalia cathartica* Thouars (Figs. 25–28, 131)

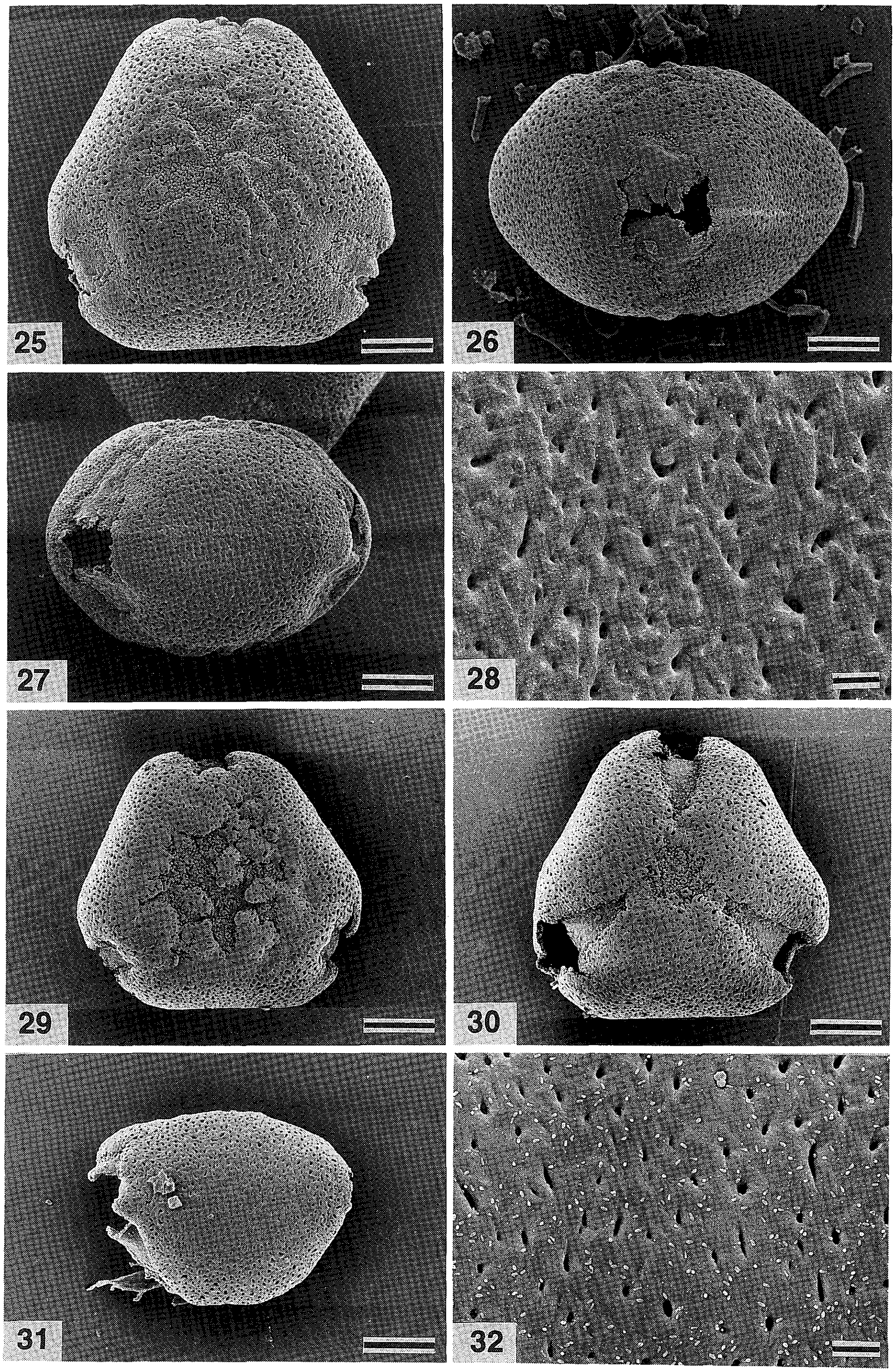
Pollen grains tricolporate, heteropolar; (30.6–)32.2(–34.2) µm in polar axis, (41.4–) 46.9(–52.2) µm in equatorial diameter; P/E = (0.61–)0.69(–0.80), oblate to suboblate in shape, circular to rhomboidal in equatorial view, subangular in polar view. Colpi 0.6–0.7 times the length of the polar axis, 25–29.2 × 3–7 µm, narrowing slightly to rounded or rectangular ends toward the pole with large apocolpium and narrowing slightly to rounded or subacute ends towards the pole with small apocolpium, colpus



Figs. 9–16. SEM micrographs of pollen of *Mucuna gigantea* (9–12) and *M. macrocarpa* (13–16). 9, 13: Polar view. 10, 14: Equatorial view showing aperture. 11, 15: Equatorial view showing mesocolpium. 12, 16: Enlargement of mesocolpium. Scales = 10 μm (9–11, 13–15), 1 μm (12, 16).



Figs. 17–24. SEM micrographs of pollen of *Mucuna membranacea* (17–20) and *M. sempervirens* (21–24). 17, 21: Polar view. 18, 22: Equatorial view showing aperture. 19, 23: Equatorial view showing mesocolpium. 20, 24: Enlargement of mesocolpium. Scales = 10 μm (17–19, 21–23), 1 μm (20, 24).



Figs. 25–32. SEM micrographs of pollen of *Canavalia cathartica* (25–28) and *C. lineata* (29–32). 25, 29, 30: Polar view. 26: Equatorial view showing aperture. 27, 31: Equatorial view showing mesocolpium. 28, 32: Enlargement of mesocolpium. Scales = 10 μm (25–27, 29–31), 1 μm (28, 32).

membrane ±smooth or partly with verrucae or granules, margins undifferentiated from the mesocolpium or with a ±complete tectum; endoaperture lalongate, 9.1–12.5 × 14–17.5 µm. Sexine semitectate; mesocolpium perforate with rugulate sculpture on the surface; apocolpia verrucate to perforate to granulate.

(8) *Canavalia lineata* (Thunb.) DC. (Figs. 29–32, 132)

Pollen grains tricolporate, heteropolar; 30–34 µm in polar axis, (40.0–)43.4(–47.5) µm in equatorial diameter, P/E = ca.0.58, oblate in shape, circular to rhomboidal in equatorial view, subangular in polar view. Colpi 0.7–0.8 times the length of polar axis, ca. 25 × 3.3–8 µm, narrowing slightly to rounded or rectangular ends toward the pole with large apocolpium and narrowing slightly towards the pole with small apocolpium and fusing to each other, colpus membrane ±smooth or with granules, margins undifferentiated from the mesocolpium; endoaperture lalongate, 4.1–5.9 × 11.6–14.2 µm. Sexine semitectate, mesocolpium perforate with rugulate sculpture on the surface; apocolpia different in sculpture between two poles, verrucate-perforate-granulate in one pole and granulate in the other.

(9) *Canavalia rosea* (Sw.) DC. (Figs. 33–36, 133)

Pollen grains tricolporate, heteropolar; (35.0–)40.1(–43.8) µm in polar axis, (47.5–)53.8(–58.8) µm in equatorial diameter; P/E = (0.65–)0.75(–0.81), oblate to suboblate in shape, circular to rhomboidal in equatorial view, subangular in polar view. Colpi 0.7–0.8 times the length of polar axis, 29–34 × 4.1–6.7 µm, narrowing slightly to rounded or rectangular ends toward the pole with large apocolpium and narrowing slightly to subacute ends towards the pole with small apocolpium, colpus membrane ±smooth or with granules, margins undifferentiated from the mesocolpium; endoaperture lalongate, ca. 8 × 12 µm. Sexine semitectate; mesocolpium perforate with slightly rugulate sculpture on the surface; apocolpia different in sculpture between two poles, verrucate to perforate to granulate in one pole and granulate in the other.

(10) *Galactia tashiroi* Maxim. (Figs. 37–40, 134)

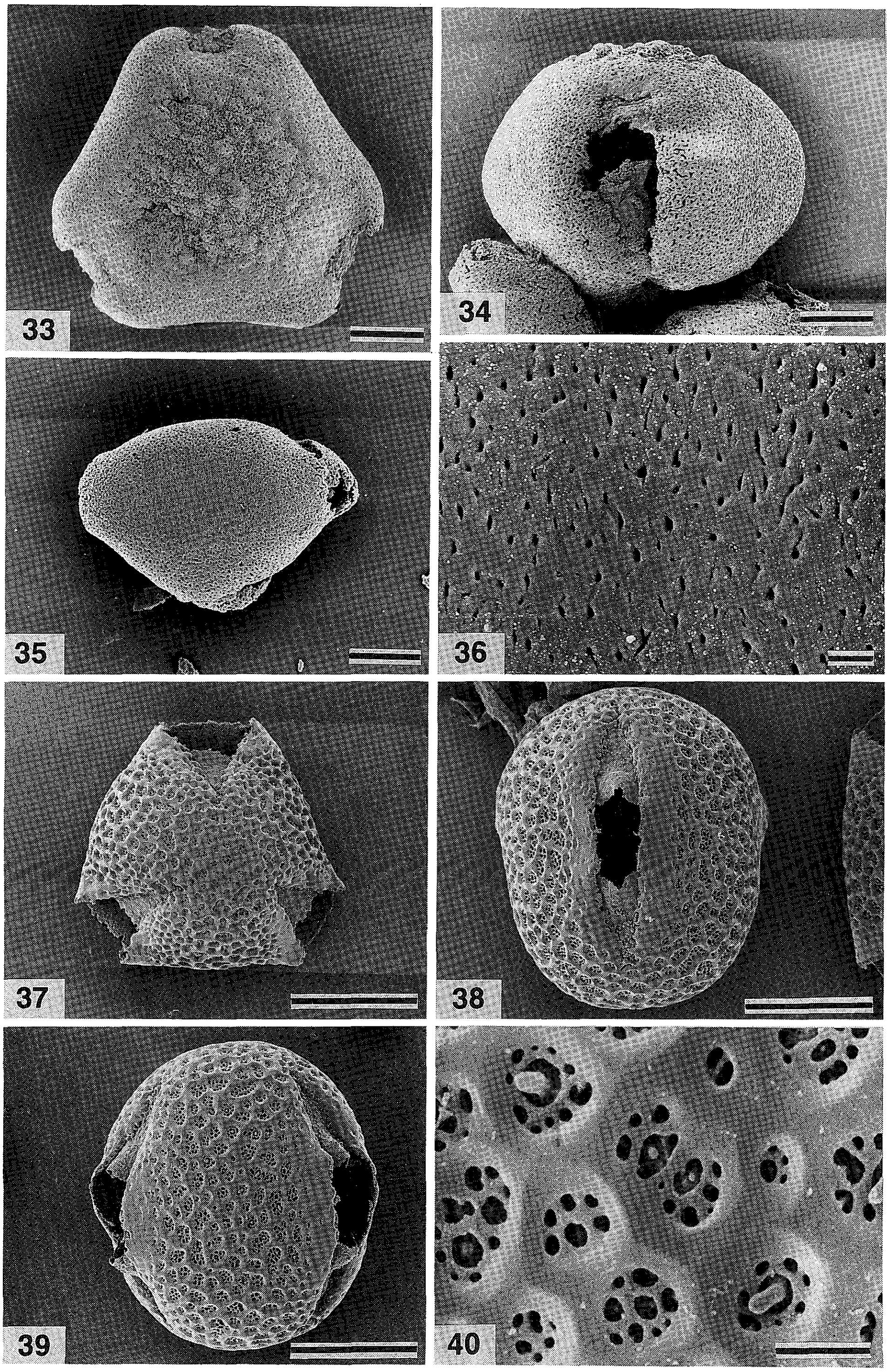
Pollen grains tricolporate; (22.5–)25.3(–27.5) µm in polar axis, (20.0–)21.3(–25.0) µm in equatorial diameter; P/E = (1.00–)1.19(–1.38), prolate spheroidal to prolate in shape, circular in equatorial view, semiangular in polar view. Colpi ca. 0.7 times the length of polar axis, 18.3–19.2 × 2–5 µm, narrowing to pointed ends, colpus membrane granulate or smooth, margins with a complete tectum; endoaperture lolongate, 5.8–7.5 × 3–7 µm. Sexine semitectate; mesocolpium reticulate to fine reticulate; muri 0.3–0.7 µm width, ridge-shaped; lumina 0.7–1.2 µm in diameter, with fine reticulate sculpture.

(11) *Amphicarpaea bracteata* (L.) Fernald subsp. *edgeworthii* (Benth.) H. Ohashi (Figs. 41–44, 135)

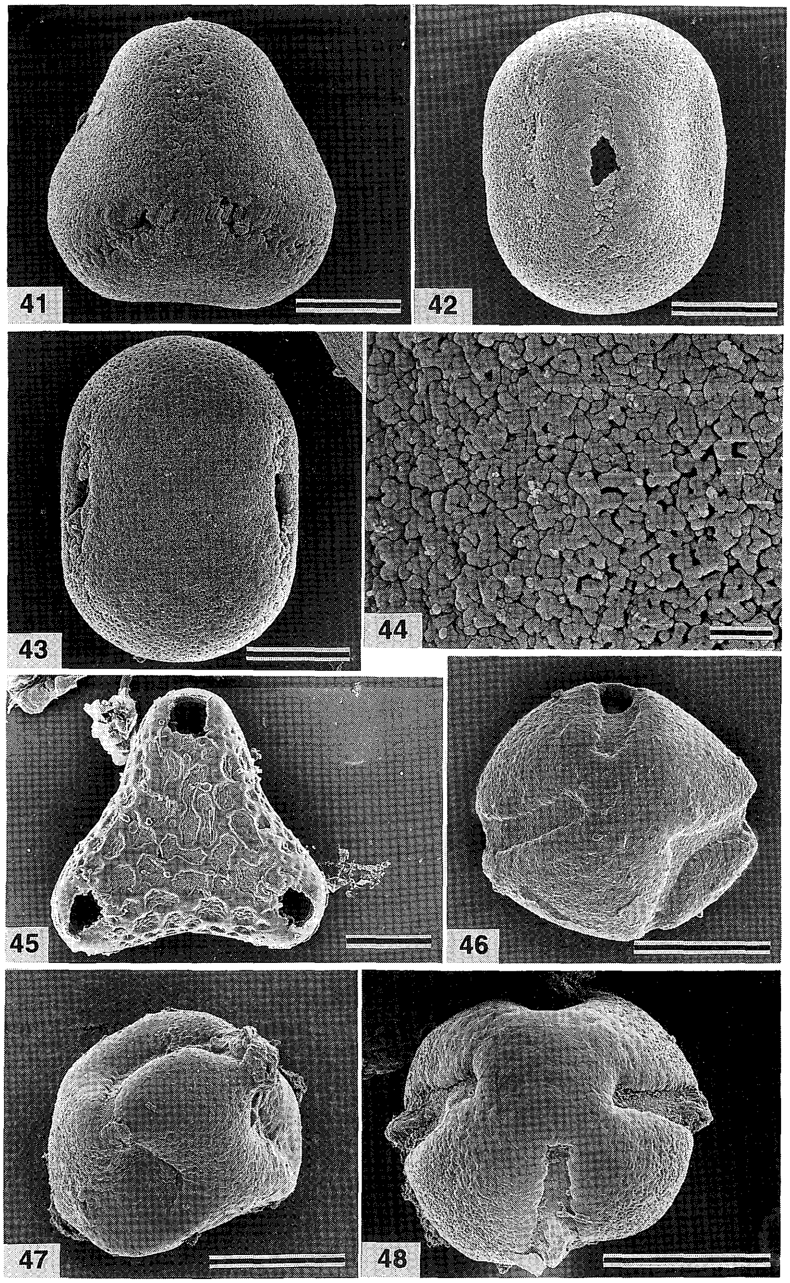
Pollen grains tricolporate; (25.2–)26.9(–30.6) µm in polar axis, (19.8–)21.2(–30.6) µm in equatorial diameter; P/E = (0.94–)1.28(–1.45), oblate spheroidal to prolate in shape, circular to compressed oval in equatorial view, circular to subangular in polar view. Colpi poorely developed, ca. 0.5 times the length of polar axis, ca. 14.5 × 3 µm, colpus membrane verrucate, margins undifferenciated from the mesocolpium; endoaperture lolongate to circular, 5–8.4 × 3.3–6.3 µm. Sexine semitectate; mesocolpium granulate to rugulate.

(12) *Dumasia truncata* Siebold & Zucc. (Figs. 45, 136, 137)

Pollen grains hexaporate (with three aper-



Figs. 33–40. SEM micrographs of pollen of *Canavalia rosea* (33–36) and *Galactia tashiroi* (37–40). 33, 37: Polar view. 34, 38: Equatorial view showing aperture. 35, 39: Equatorial view showing mesocolpium. 36, 40: Enlargement of mesocolpium. Scales = 10 μm (33–35, 37–39), 1 μm (36, 40).



Figs. 41–48. SEM micrographs of pollen of *Amphicarpaea bracteata* subsp. *edgeworthii* (41–44), *Dumasia truncata* (45) and *Glycine koidzumii* (46–48). 41, 45, 48: Polar view. 42: Equatorial view showing aperture. 43: Equatorial view showing mesocolpium. 44: Enlargement of mesocolpium. 46, 47: Scales = 10 µm (41–43, 45–48), 1 µm (44).

tures composed of two pores); 16–25 μm in polar axis, (32.5–)34.7(–40.0) μm in equatorial diameter, P/E = 0.43–0.65, peroblate to oblate in shape, depressed oval in equatorial view, angular, lobate or semilobate in polar view. Pores angular, circular or lalongate, 2.5–6 × 6–9 μm; annuli with a complete tectum and smooth. Sexine semitectate; mesocolpium reticulate and apocolpium coarsely reticulate; muri 0.3–1.5 μm width in mesocolpium and 0.6–2.5 μm width in apocolpium; lumina circular, 1–3 μm in diameter in mesocolpoium and irregularly angular, 3–9 μm width inapocolpium, with slightly verrucate to rugulate sculpture.

(13) *Glycine koidzumii* Ohwi (Figs. 46–48)

Pollen grains tri- or tetra-colporate; ca. 15–18 μm in equatorial diameter; outlines variable, more or less circular in equatorial view, more or less semiangular in polar view. Colpi inordinately arranged, variable in shape from a colpus winded (Figs. 46, 47) to straightly elongated (Fig. 48), 2.5–4 μm wide at equator, narrowing slightly to rounded ends, colpus membrane smooth or with granules, margins undifferentiated from the mesocolpium; endoaperture circular, ca. 3 μm in diameter. Sexine tectate to semitectate; mesocolpium perforate to rugulate to psilate.

(14) *Glycine max* (L.) Merr. subsp. *soja* (Siebold & Zucc.) H. Ohashi (Figs. 49–52, 140)

Pollen grains tricolporate; (17.5–)21.6 (–27.5) μm in polar axis, (16.3–)19.4(–25.0) μm in equatorial diameter; P/E = (1.00–)1.12 (–1.38), prolate spheroidal to prolate in shape, circular in equatorial view, semiangular to circular in polar view. Colpi 0.6–0.7 times the length of polar axis, 12.5–16.7 × 1.6–3.8 μm, narrowing slightly to rounded ends, colpus membrane granulate, margins with a complete tectum, smooth; endoaperture circular to subcircular, 3.3–5 × 3.3–4.6 μm. Sexine semitectate; mesocolpium reticulate to rugulate, lumina 0.6–1.7 μm in diameter with fine granulate to verrucate sculpture; apocolpium psilate.

(15) *Glycine tabacina* (Labill.) Benth. (Figs. 53–56)

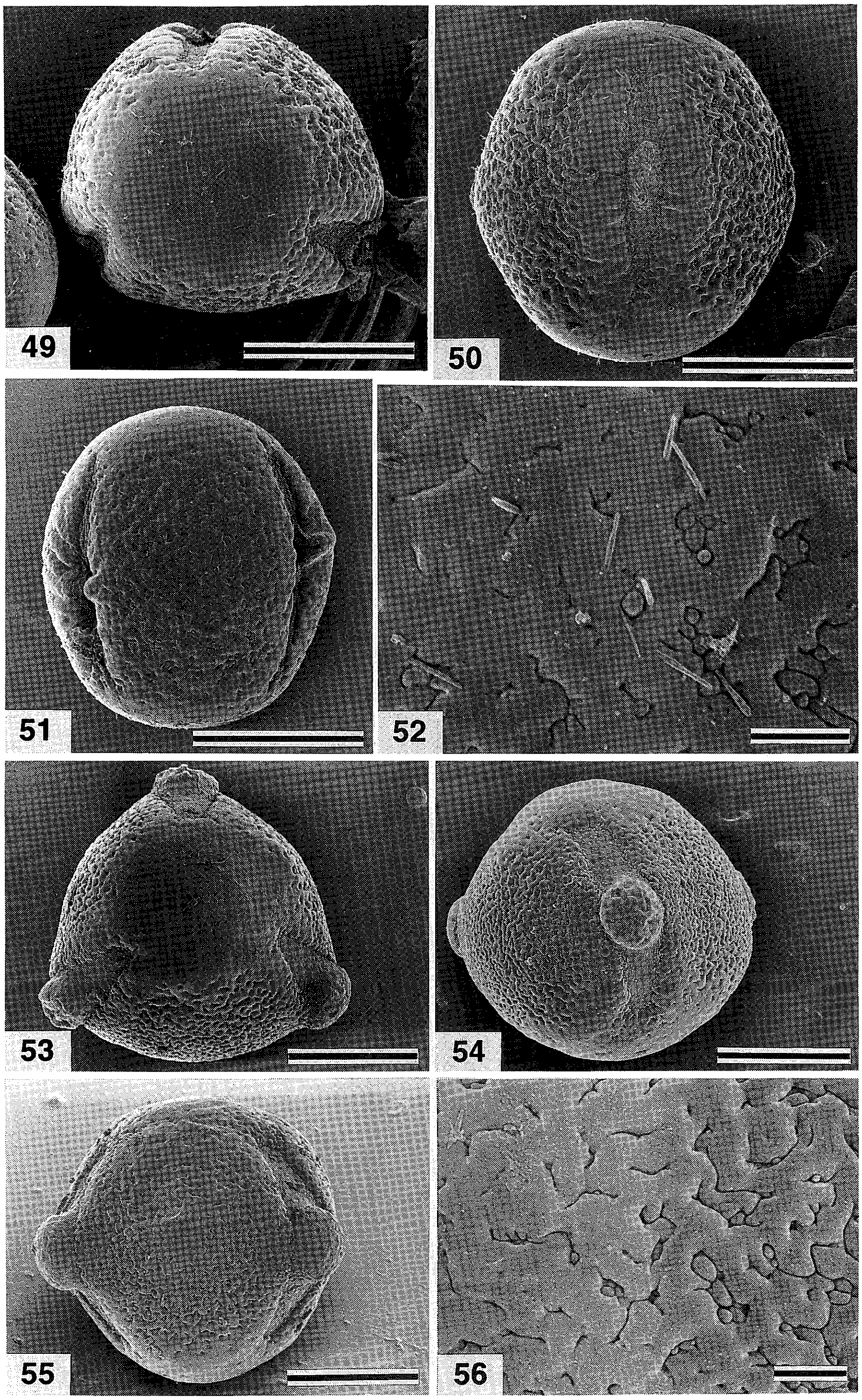
Pollen grains tricolporate; 21–23 μm in polar axis, 21–23 μm in equatorial diameter; P/E = ca. 1.0, oblate spheroidal to prolate spheroidal in shape, circular in equatorial view, semiangular in polar view. Colpi ca. 0.65 times the length of polar axis, 14.4–17.5 × 3.9–5.5 μm, narrowing slightly to rounded ends, colpus membrane ±smooth or ±granulate; margins undifferentiated from the mesocolpium, endoaperture circular, ca. 5.5 in diameter. Sexine semitectate; mesocolpium reticulate to rugulate, muri 0.3–0.7 μm wide, lumina 0.3–1.1 μm in diameter with fine granulate to verrucate sculpture; apocolpium psilate.

(16) *Pueraria lobata* (Willd.) Ohwi (Figs. 57–60, 138)

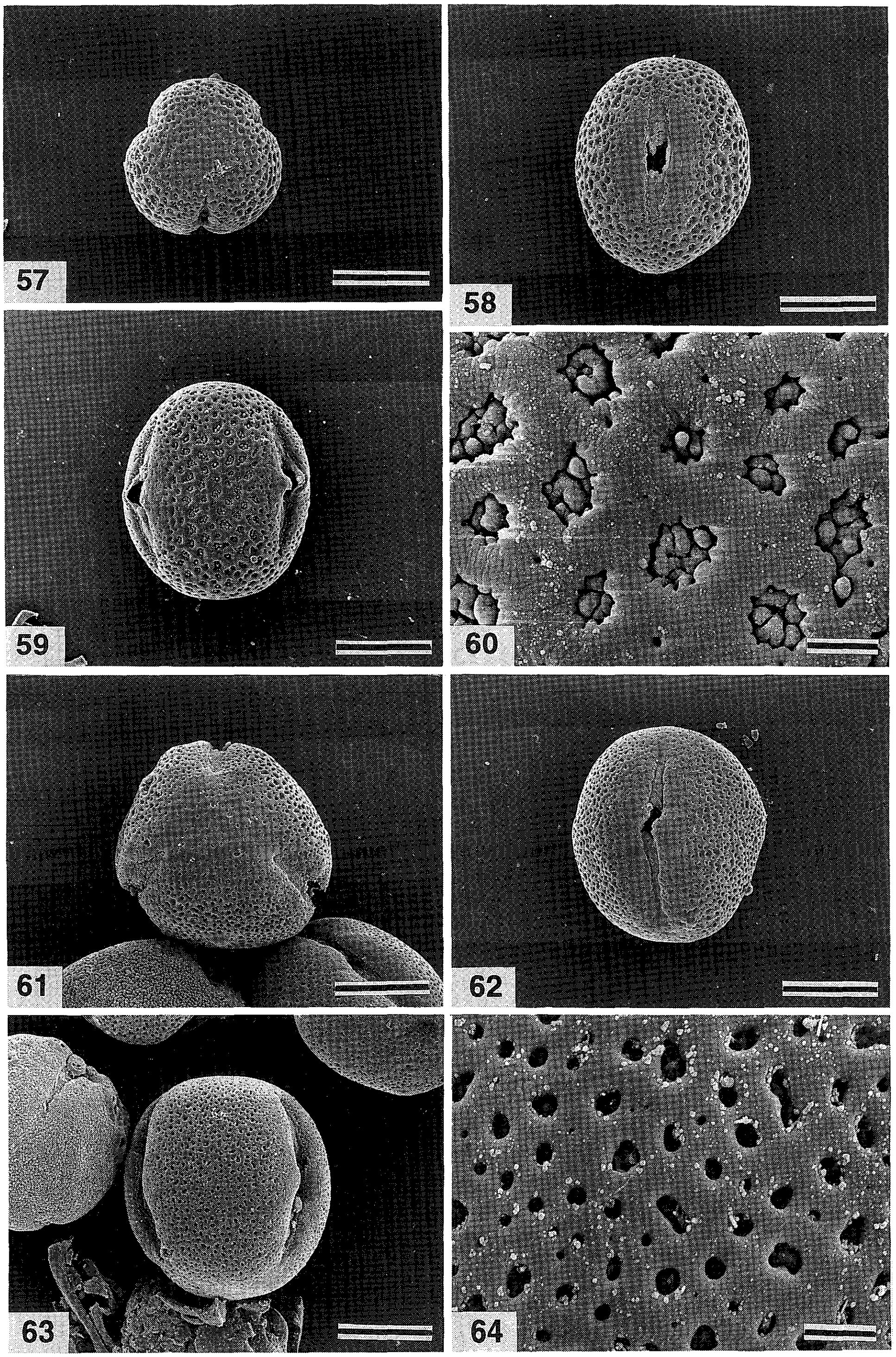
Pollen grains tricolporate; (21.6–)25.7 (–29.7) μm in polar axis, (18.0–)20.6(–23.4) μm in equatorial diameter; P/E = (1.08–)1.25 (–1.36), prolate spheroidal to prolate in shape, subcircular in equatorial view, semiangular to circular in polar view. Colpi ca. 0.6 times the length of polar axis, 14–16 × 1.6–3.3 μm, narrowing slightly to pointed ends, colpus membrane smooth and partly granulate, margins undifferentiated from the mesocolpium or ±smooth and a little pitted; endoaperture circular to lolongate, 7.5–8.3 × 7.5–8.3 μm. Sexine semitectate; mesocolpium reticulate; muri 0.6–1.5 μm wide, with slightly rugulate sculpture; lumina 0.8–1.7 μm in diameter, with granules.

(17) *Pueraria montana* (Lour.) Merr. (Figs. 61–64, 139)

Pollen grains tricolporate; (21.6–)23.0



Figs. 49–56. SEM micrographs of pollen of *Glycine max* subsp. *soja* (49–52) and *G. tabacina* (53–56). 49, 53: Polar view. 50, 54: Equatorial view showing aperture. 51, 55: Equatorial view showing mesocolpium. 52, 56: Enlargement of mesocolpium. Scales = 10 μm (49–51, 53–55), 1 μm (52, 56).



Figs. 57–64. SEM micrographs of pollen of *Pueraria lobata* (57–60) and *P. montana* (61–64). 57, 61: Polar view. 58, 62: Equatorial view showing aperture. 59, 63: Equatorial view showing mesocolpium. 60, 64: Enlargement of mesocolpium. Scales = 10 μm (57–59, 61–63), 1 μm (60, 64).

(–25.2) µm in polar axis, (18.0–)19.7(–21.6) µm in equatorial diameter; P/E = (1.08–)1.17 (–1.30), prolate spheroidal to subprolate in shape, circular in equatorial view, circular to semiangular in polar view. Colpi ca. 0.7–0.8 times the length of polar axis, 16.2–17.5 × 1.4–2.3 µm, narrowing slightly to pointed ends, colpus membrane ±smooth or partly verrucate, margins undifferentiated from the mesocolpium or ±smooth and a little pitted; endoaperture circular to lolongate, 5–8.3 × 3.3–5.9 µm. Sexine semitectate; mesocolpium reticulate to perforate; muri 0.3–0.9 µm wide, smooth; lumina 0.1–0.8 µm in diameter.

(18) *Vigna angularis* (Willd.) Ohwi & H. Ohashi var. *nipponensis* (Ohwi) Ohwi & H. Ohashi (Figs. 65–68, 141)

Pollen grains triporate; (27.5–)33.4(–37.5) µm in polar axis, (32.5–)36.5(–42.5) µm in equatorial diameter; P/E = (0.85–)0.92 (–1.00), suboblate to oblate spheroidal in shape, circular in equatorial view, semiangular to circular in polar view. Pores lalongate to circular to lolongate, 5–8.3 µm in diameter; annuli with several exinous globules. Sexine semitectate; mesocolpium reticulate; muri 0.6–0.9 µm wide, smooth and ridge-shaped; lumina tetragonal to octagonal (in many cases pentagonal or hexagonal), variable in size, brochi 3.3–13.0 µm wide, perforate to rugulate.

(19) *Vigna minima* (Roxb.) Ohwi & H. Ohashi var. *minor* (Matsum.) Tateishi (Figs. 69–72, 142)

Pollen grains triporate; (32.5–)35.7(–40.0) µm in polar axis, (37.5–)38.7(–42.5) µm in equatorial diameter; P/E = (0.85–)0.92 (–1.00), suboblate to oblate spheroidal in shape, circular in equatorial view, semiangular to circular in polar view. Pores lalongate to circular to lolongate, 5.4–9.2 µm in diameter; annuli with several exinous globules. Sexine semitectate; mesocolpium reticulate; muri ca. 0.3 µm wide, smooth ridge-shaped, sometimes disappearing halfway; lumina tetragonal to octagonal (in many cases pentagonal or hexagonal), variable in size, brochi 3.6–20 µm in diameter, perforate to rugulate.

(20) *Vigna minima* (Roxb.) Ohwi & H. Ohashi var. *minima* (= *Vigna nakashimae* (Ohwi) Ohwi & H. Ohashi) (Figs. 73–76, 143)

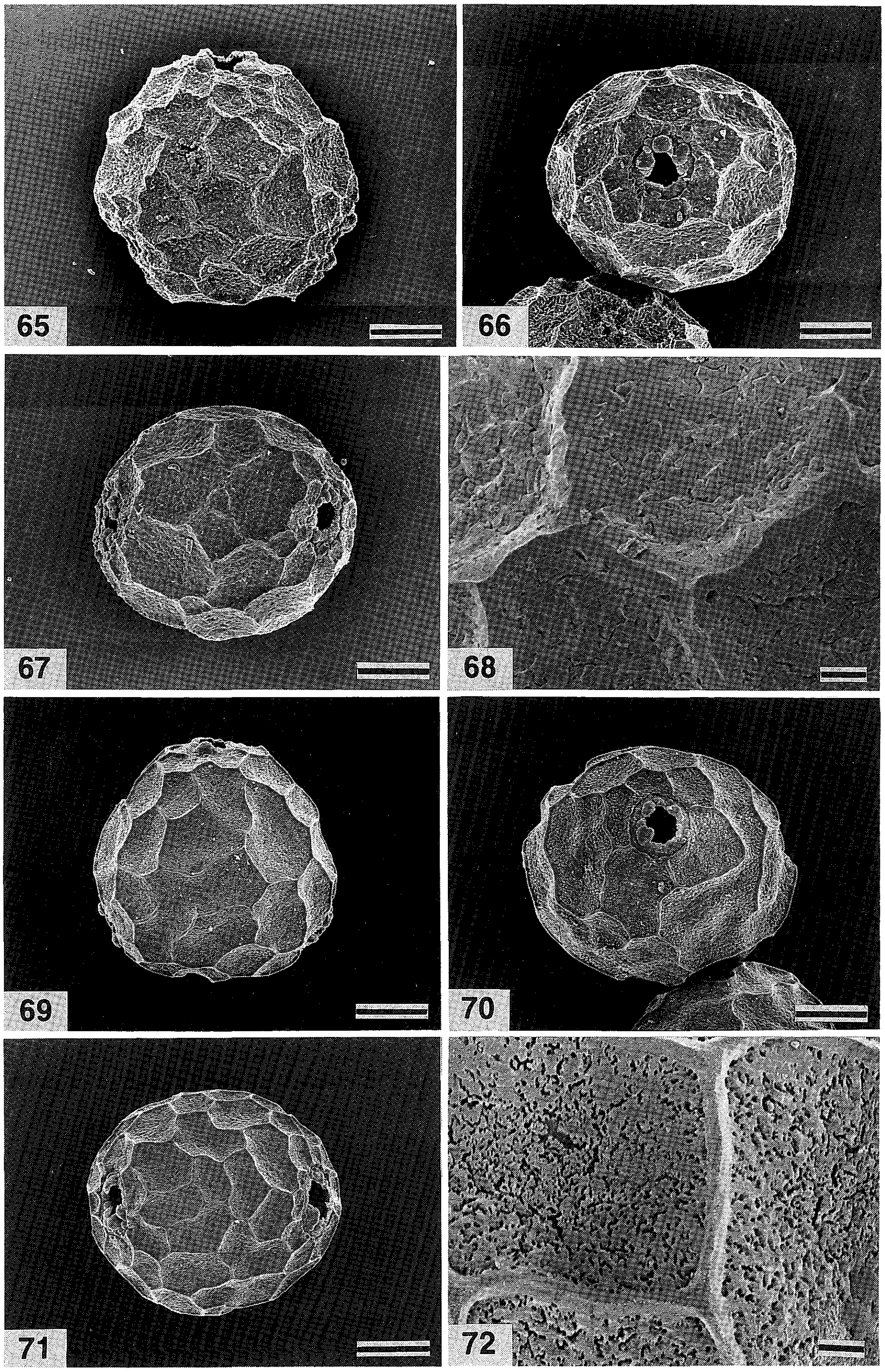
Pollen grains triporate; (22.5–)25.7(–30.0) µm in polar axis, (27.5–)29.8(–32.5) µm in equatorial diameter; P/E = (0.69–)0.86 (–1.00), oblate to oblate spheroidal in shape, circular in equatorial view, semiangular to circular in polar view. Pores lalongate to circular to lolongate, 4.2–5.5 µm in diameter; annuli with several exinous globules. Sexine semitectate; mesocolpium reticulate; muri ca. 0.4 µm wide, smooth, ridge-shaped; lumina tetragonal to octagonal (in many cases pentagonal or hexagonal), variable in size, brochi 2.7–17 µm wide, perforate to rugulate.

(21) *Vigna reflexopilosa* Hayata (Figs. 77–80, 144)

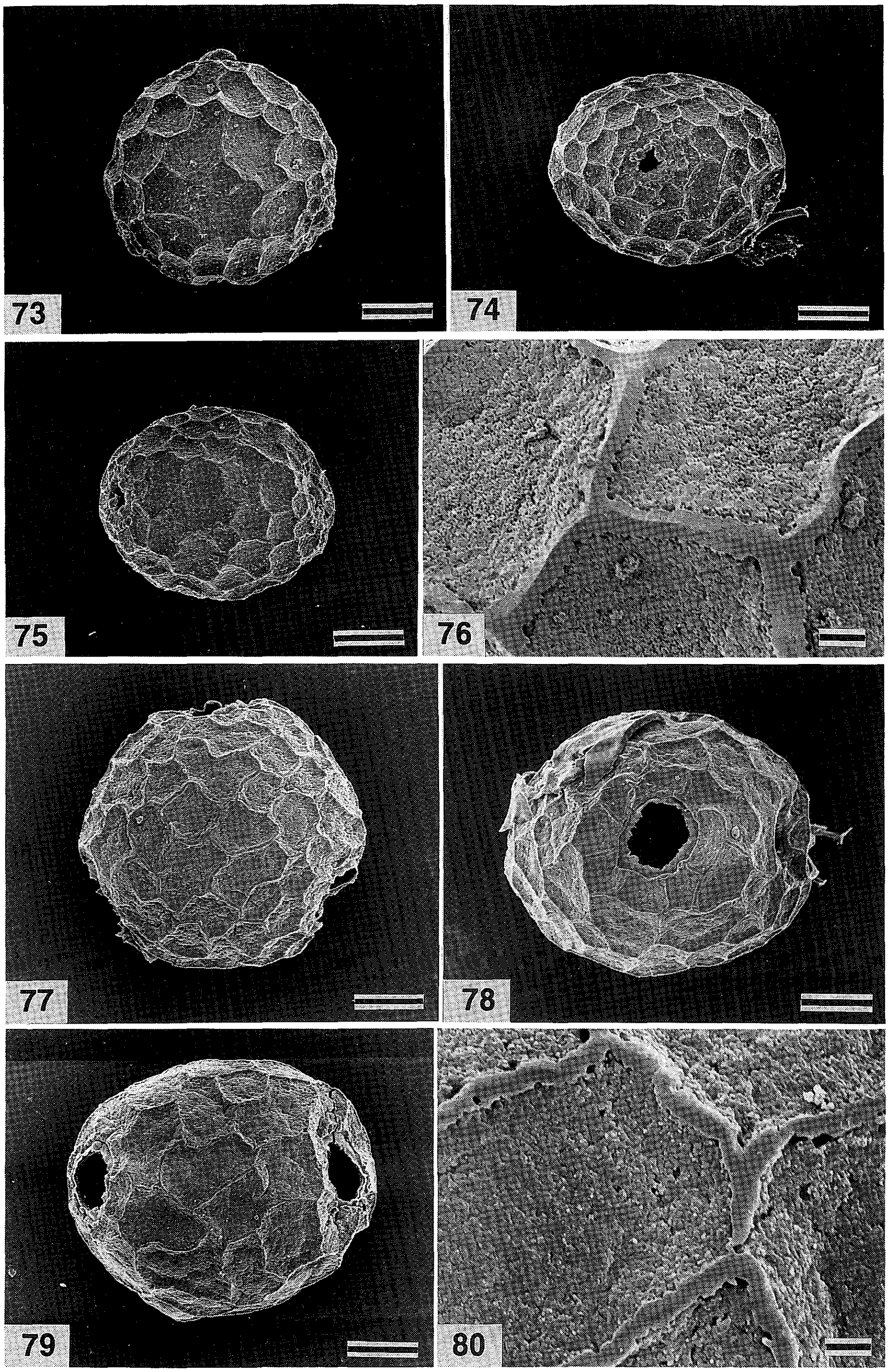
Pollen grains tri(–tetra)porate; (27.5–)37.1 (–42.5) µm in polar axis, (32.5–)41.5(–52.5) µm in equatorial diameter; P/E = (0.73–)0.89 (–1.00), oblate to oblate spheroidal in shape, circular in equatorial view, semiangular to circular in polar view. Pores lalongate to circular to lolongate, 5.8–10 µm in diameter; annuli with several exinous globules. Sexine semitectate, mesocolpium reticulate; muri ca. 0.4 µm wide, smooth; lumina tetragonal to octagonal (in many cases pentagonal or hexagonal), variable in size, 4–18.5 µm in diameter, rugulate.

(22) *Vigna vexillata* (L.) A. Rich. var. *vexillata* (Figs. 81–84, 145)

Pollen grains triporate; (40.0–)54.8(–72.5) µm in polar axis, (45.0–)62.7(–87.5) µm in



Figs. 65–72. SEM micrographs of pollen of *Vigna angularis* var. *nipponensis* (65–68) and *V. minima* var. *minor* (69–72). 65, 69: Polar view. 66, 70: Equatorial view showing aperture. 67, 71: Equatorial view showing mesocolpium. 68, 72: Enlargement of mesocolpium. Scales = 10 μm (65–67, 69–71), 1 μm (68, 72).



Figs. 73–80. SEM micrographs of pollen of *Vigna minima* var. *minima* (73–76) and *V. reflexopilosa* (77–80). 73, 77: Polar view. 74, 78: Equatorial view showing aperture. 75, 79: Equatorial view showing mesocolpium. 76, 80: Enlargement of mesocolpium. Scales = 10 μm (73–75, 77–79), 1 μm (76, 80).

equatorial diameter; P/E = (0.80–)0.88 (–1.00), suboblate to oblate spheroidal in shape, circular in equatorial view, semiangular to circular in polar view. Pores circular, 7.5–15 μm in diameter; annuli with granules. Sexine semitectate; mesocolpium reticulate; muri 0.5–1 μm wide, smooth; lumina tetragonal to octagonal but often pentagonal or hexagonal, variable in size, 10–28.5 μm in diameter, rugulate-granulate.

(23) *Vigna adenantha* (G. F. Meyer) Maréchal, Mascherpa & Stainier (Figs. 85–88, 146)

Pollen grains tricolporate; (20.0–)22.4 (–25.0) μm in polar axis, (30.0–)31.5(–35.0) μm in equatorial diameter; P/E = (0.64–)0.71 (–0.83), oblate to suboblate in shape, circular to rhomboidal in equatorial view, semiangular in polar view. Colpi lolongate, 0.6–0.7 times the length of polar axis, 16.6 × 8–10.8 μm, narrowing slightly to rounded ends, colpus membrane with granules, margins with a complete tectum; endoaperture circular, 4–6.6 μm in diameter. Sexine semitectate, mesocolpium verrucate to granulate.

(24) *Vigna luteola* (Jacq.) Benth. (Figs. 89–92, 147)

Pollen grains triporate; (32.5–)34.9(–37.5) μm in polar axis, (37.5–)39.3(–42.5) μm in equatorial diameter; P/E = (0.81–)0.89 (–0.94), suboblate to oblate spheroidal in shape, circular in equatorial view, semiangular to circular in polar view (in many cases semiangular). Pores lolongate, 7.5–9.1 × 5–6.6 μm; annuli with a more or less complete tectum. Sexine semitectate; mesocolpium reticulate; muri ca. 0.5 μm wide, smooth; lumina tetragonal to octagonal but often pentagonal or hexagonal, variable in size, 3.0–7.0 μm in diameter, verrucate to perforate.

(25) *Vigna marina* (Burm. f.) Merr. (Figs. 93–96, 148)

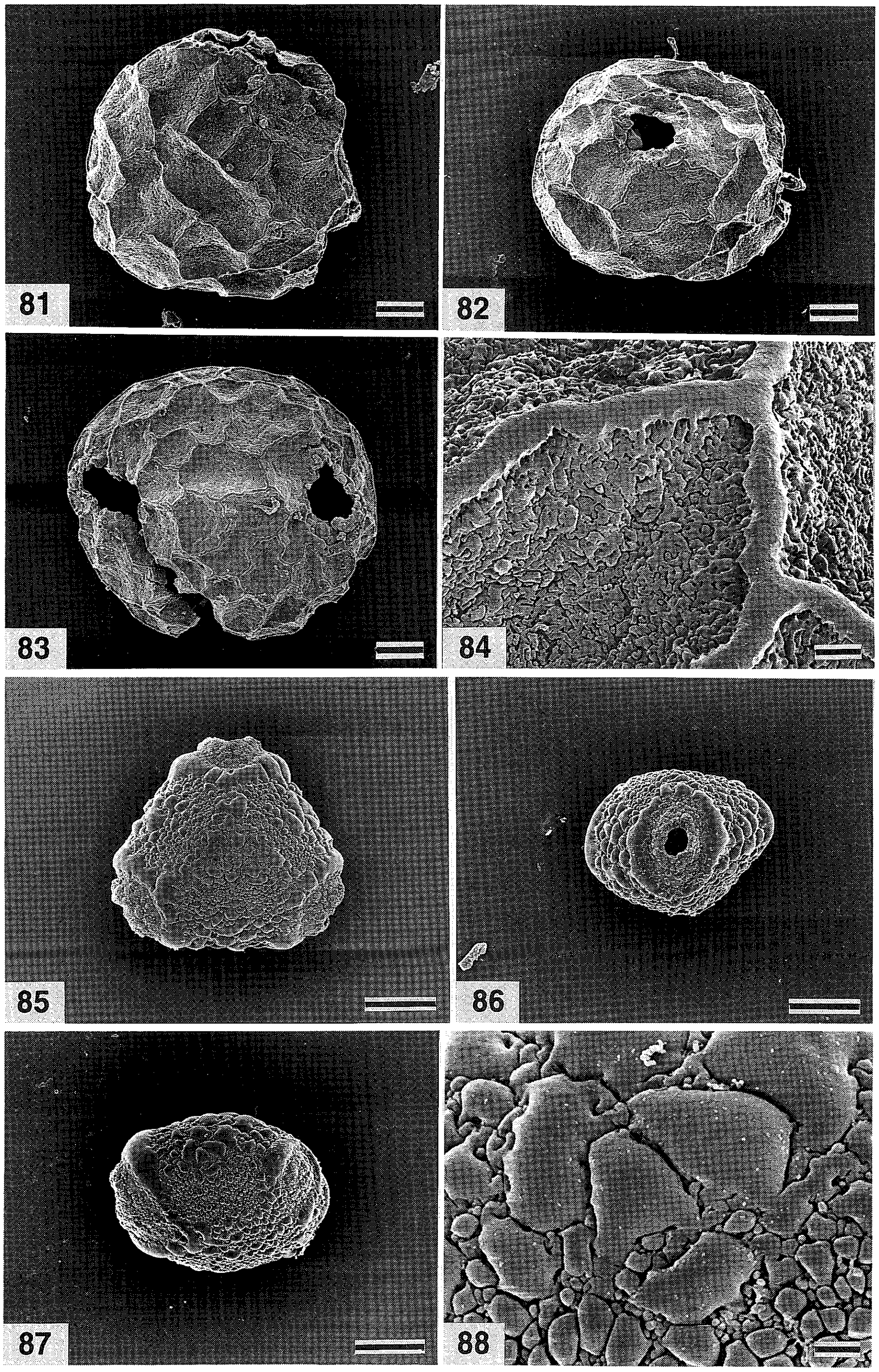
Pollen grains triporate; (27.5–)30.3(–35.0) μm in polar axis, (27.5–)34.8(–42.5) μm in equatorial diameter; P/E = (0.76–)0.87 (–1.00), suboblate to oblate spheroidal in shape, circular in equatorial view, semiangular to circular in polar view. Pores circular, (4.2–)5.0–7.5(–8.3) μm in diameter; annuli with several exinous globules. Sexine semitectate; mesocolpium reticulate; muri ca. 0.3 μm wide, sometimes disappearing halfway; lumina 0.9–2.1 μm in diameter, verrucate.

(26) *Cajanus scarabaeoides* (L.) Thouars (Figs. 97–100, 149)

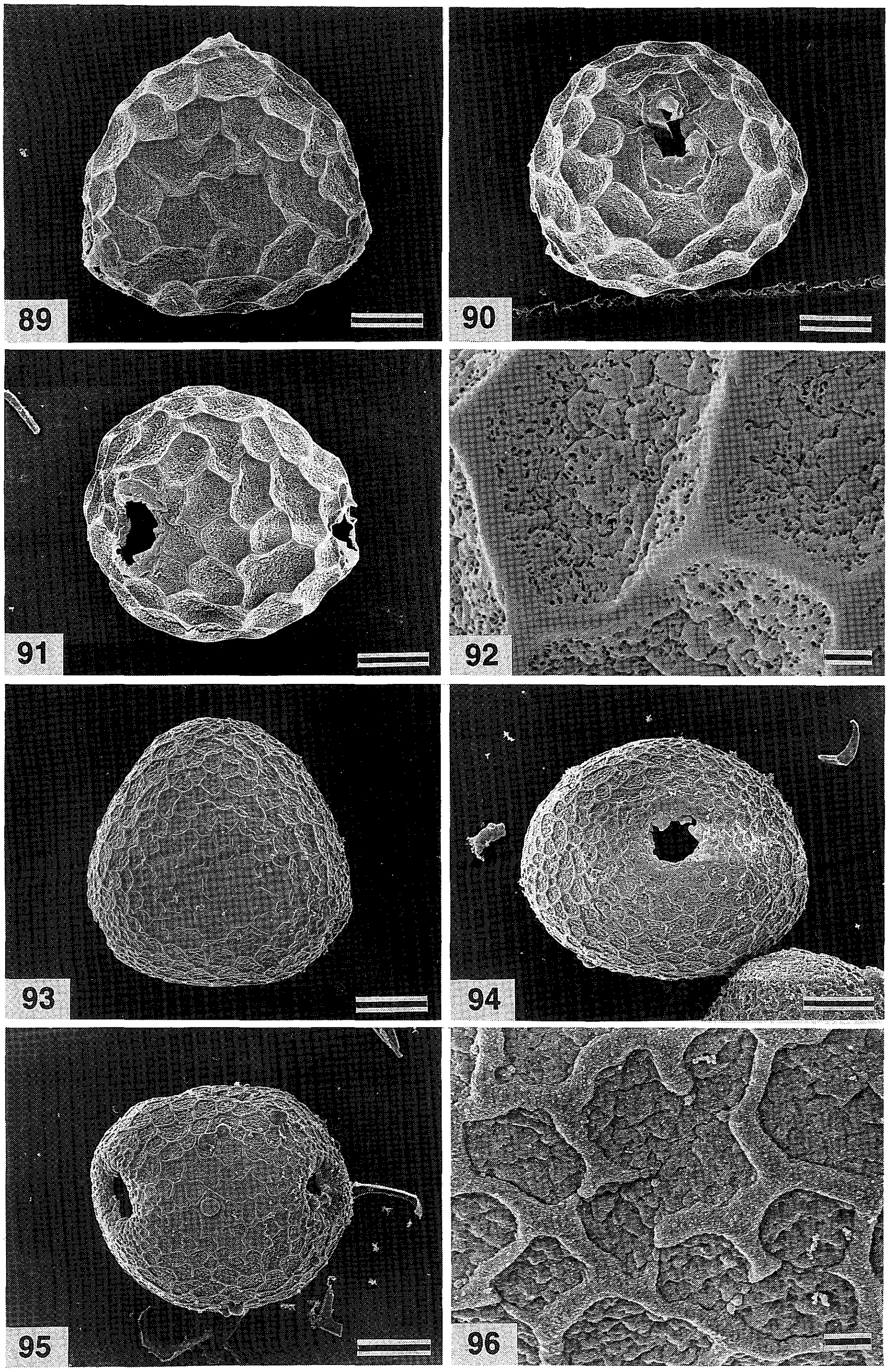
Pollen grains tricolporate; (25.0–)28.4 (–35.0) μm in polar axis, (23.8–)26.8(–32.5) μm in equatorial diameter; P/E = (0.91–)1.06 (–1.20), oblate spheroidal to subprolate in shape, circular in equatorial view, semiangular in polar view. Colpi 0.7–0.8 times the length of polar axis, 19–20.5 × 2.3–3.6 μm, narrowing to pointed or rounded ends, colpus membrane granulate to verrucate; margins with a complete tectum; endoaperture lalongate to circular, 4–5 × 3.3–5 μm. Sexine semitectate; mesocolpium reticulate; muri 0.3–0.8 μm wide, smooth; lumina 0.7–1.8 μm in diameter, with granules.

(27) *Dunbaria villosa* (Thunb.) Makino (Figs. 101–104, 150)

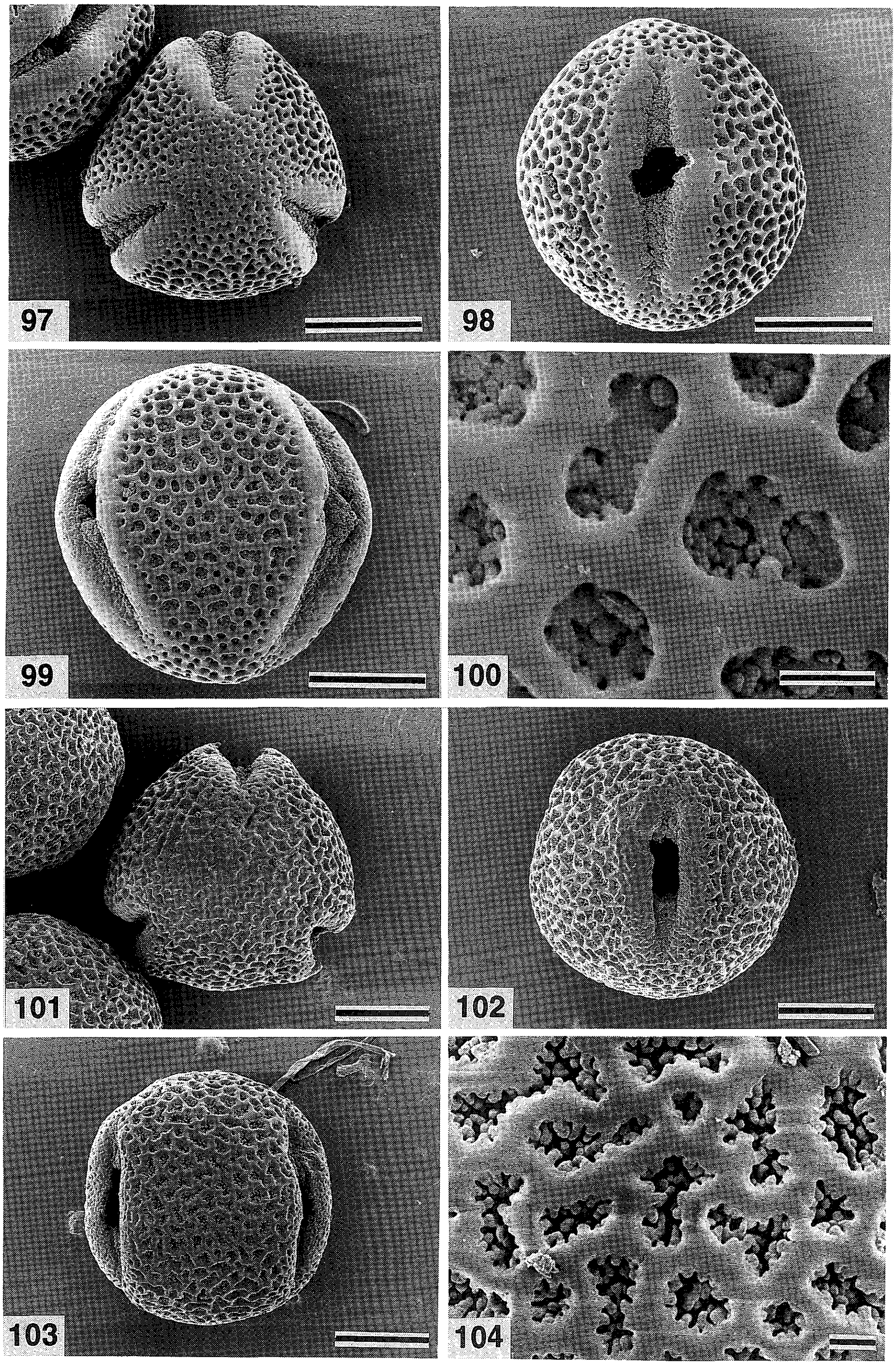
Pollen grains tricolporate; (25.0–)29.9 (–37.5) μm in polar axis, (25.0–)29.4(–35.0) μm in equatorial diameter; P/E = (0.92–)1.02 (–1.18), oblate spheroidal to subprolate in shape, circular in equatorial view, semiangular in polar view. Colpi medium to long, 0.4–0.6 times the length of polar axis, 12.5–15 × 2.9–4.5 μm, narrowing slightly to rounded ends, colpus membrane granulate to verrucate; endoaperture circular, 5.8–6.7 μm in diameter. Sexine semitectate; mesocolpium reticulate; muri 0.6–1 μm wide,



Figs. 81–88. SEM micrographs of pollen of *Vigna vexillata* var. *vexillata* (81–84) and *V. adenantha* (85–88). 81, 85: Polar view. 82, 86: Equatorial view showing aperture. 83, 87: Equatorial view showing mesocolpium. 84, 88: Enlargement of mesocolpium. Scales = 10 μm (81–83, 85–87), 1 μm (84, 88).



Figs. 89–96. SEM micrographs of pollen of *Vigna luteola* (89–92) and *V. marina* (93–96). 89, 93: Polar view. 90, 94: Equatorial view showing aperture. 91, 95: Equatorial view showing mesocolpium. 92, 96: Enlargement of mesocolpium. Scales = 10 μm (89–91, 93–95), 1 μm (92, 96).



Figs. 97–104. SEM micrographs of pollen of *Cajanus scarabaeoides* (97–100) and *Dunbaria villosa* (101–104). 97, 101: Polar view. 98, 102: Equatorial view showing aperture. 99, 103: Equatorial view showing mesocolpium. 100, 104: Enlargement of mesocolpium. Scales = 10 μm (97–99, 101–103), 1 μm (100, 104).

smooth; lumina 0.4–2 μm in diameter, with granules.

(28) *Flemingia macrophylla* (Willd.) Merr. var. *philippinensis* (Merr. & Rolfe) H. Ohashi (Figs. 105–108, 151)

Pollen grains tricolporate; (17.5–)20.7 (–23.8) μm in polar axis, (18.8–)21.2(–25.0) μm in equatorial diameter; P/E = (0.88–)0.98 (–1.13), suboblate to prolate spheroidal in shape, circular in equatorial view, circular to semiangular in polar view. Colpi 0.6–0.7 times the length of polar axis, 11.6–15 × 2.5–4.2 μm, narrowing to pointed ends, colpus membrane ±smooth and partly granulate, margins with a complete tectum; endoaperture lolongate to circular, 4.1–5.9 × 3.3–4.6 μm. Sexine semitectate; mesocolpium reticulate; muri 0.4–0.6 μm wide; lumina 0.7–2.5 μm in diameter, pitted and verucate.

(29) *Flemingia strobilifera* (L.) R. Br. (Figs. 109–112, 152)

Pollen grains tricolporate; (22.5–)26.6 (-30.0) μm in polar axis, (22.5–)27.2(-30.0) μm in equatorial diameter; P/E = (0.82–)0.98 (–1.10), suboblate to prolate spheroidal in shape, circular in equatorial view, semiangular in polar view. Colpi 0.55–0.7 times the length of polar axis, 14.6–18.6 × 4.2–8 μm, narrowing slightly to pointed ends; colpus membrane ±smooth and partly granulate, margins with a complete tectum; endoaperture circular to lolongate, 5–7.5 × 3.3–5.9 μm. Sexine semitectate; mesocolpium reticulate, partly perforate or rugulate; muri 0.25–0.8 μm wide; lumina 0.3–1.5 μm in diameter, granulate to rugulate.

(30) *Rhynchosia acuminatifolia* Makino (Figs. 113–116, 153)

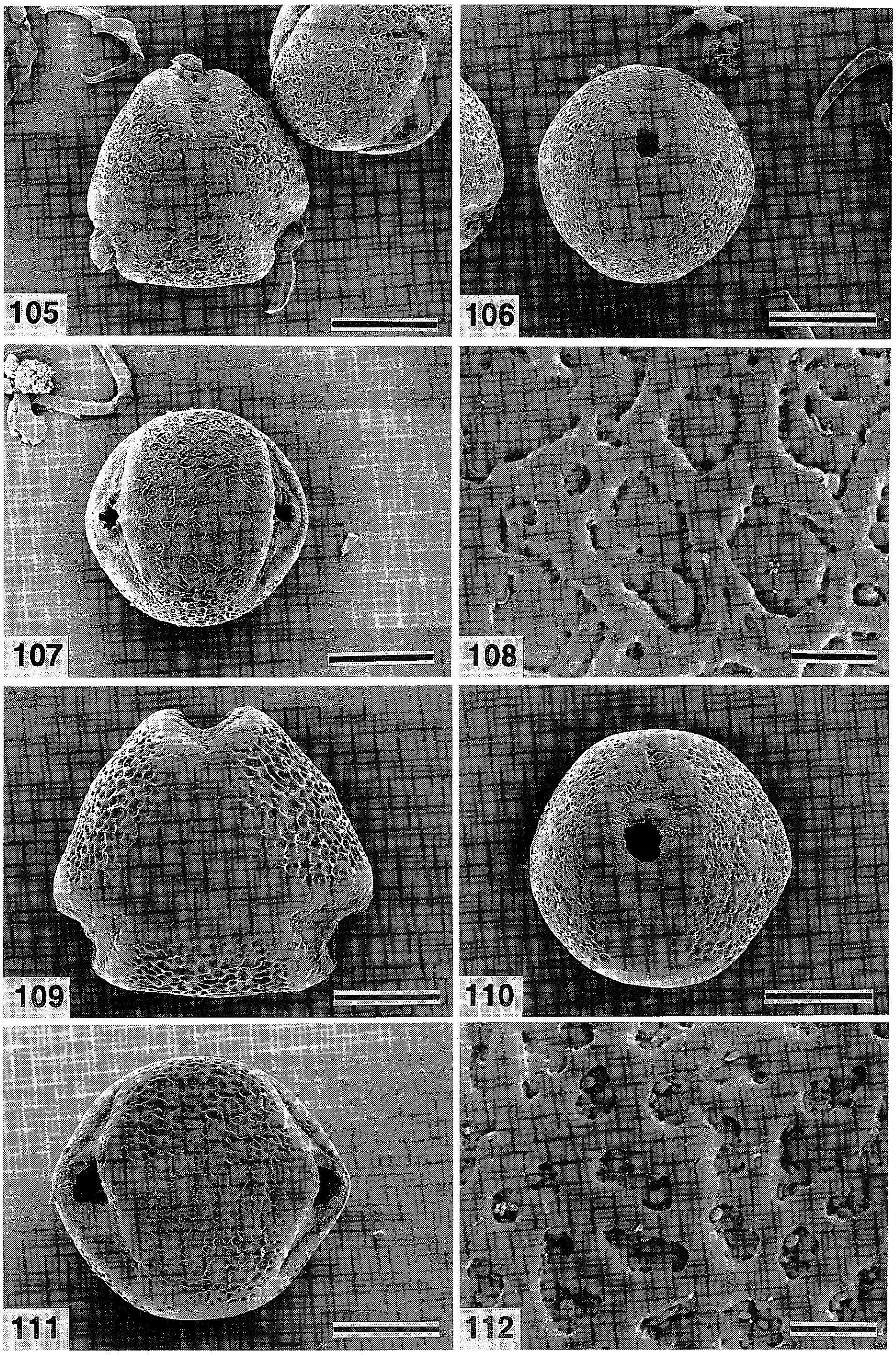
Pollen grains tricolporate, heteropolar; (19.8–)24.9(–27.0) μm in polar axis, (21.6–) 25.8(–28.8) μm in equatorial diameter; P/E = (0.92–)0.97(–1.00), oblate spheroidal in shape, circular to rhomboidal in equatorial view, semiangular in polar view. Colpi 0.4–0.6 times the length of polar axis, 12–13.5 × 3.5–5.5 μm, narrowing to rounded ends toward the pole with large apocolpium and narrowing to pointed ends towards the pole with small apocolpium, colpus membrane smooth to rugulate, margins ±smooth; endoaperture lalongate to circular to lolongate, 5.8–7.5 × 5.8–9.2 μm. Sexine semitectate; mesocolpium reticulate; muri 0.7–1.6 μm wide, smooth; lumina 0.4–0.8 μm in diameter, rugulate.

(31) *Rhynchosia minima* (L.) DC. (Figs. 117–120, 154)

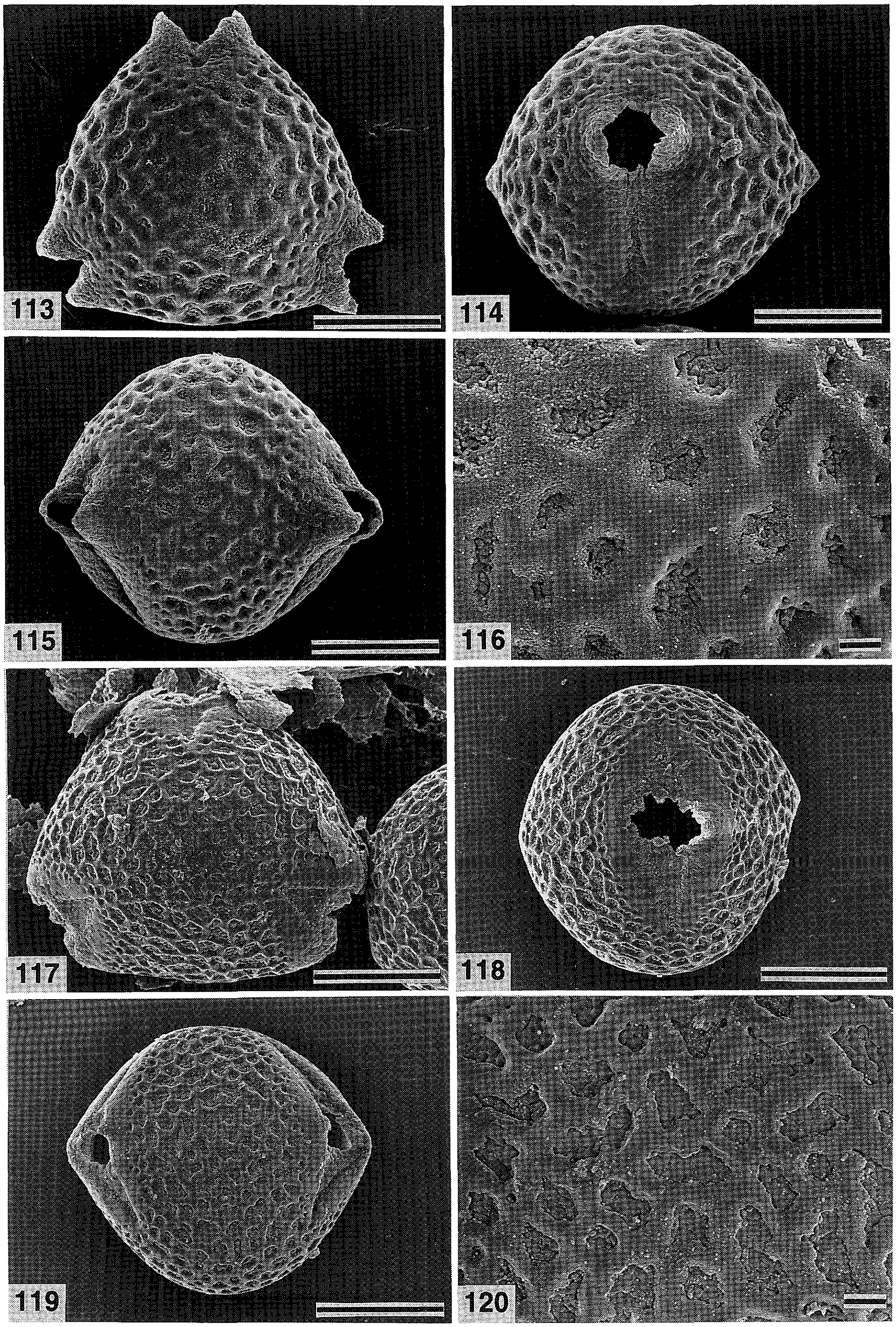
Pollen grains tricolporate, slightly heteropolar; (21.6–)23.0(–25.2) μm in polar axis, (21.6–)22.9(–27.0) μm in equatorial diameter; P/E = (0.87–)1.01(–1.08), suboblate to prolate spheroidal in shape, circular to rhomboidal in equatorial view, semiangular in polar view. Colpi 0.5–0.77 times the length of polar axis, 15–22.5 × 3.3–5 μm, narrowing to pointed ends, colpus membrane ±smooth or slightly granulate, margins with a complete tectum; endoaperture lalongate to circular to lolongate, 4.1–6.6 × 5–8.3 μm. Sexine semitectate; mesocolpium reticulate; muri ca. 0.6 μm wide, smooth; lumina 0.6–2.1 μm in diameter, rugulate.

(32) *Rhynchosia volubilis* Lour. (Figs. 121–124, 155)

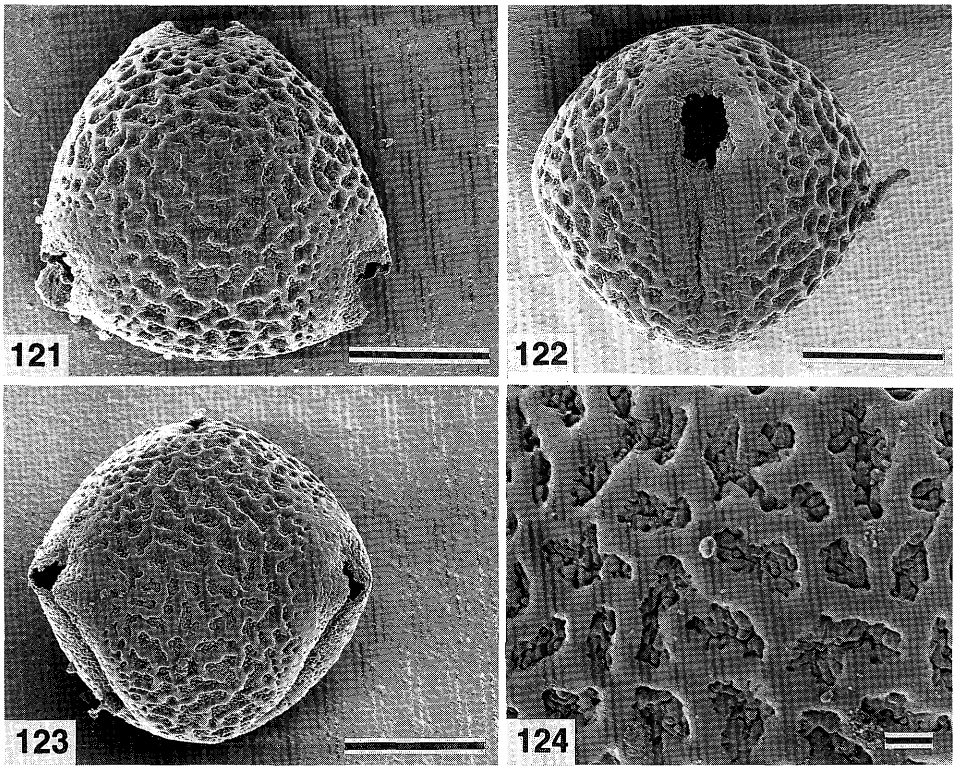
Pollen grains tricolporate, heteropolar; (17.5–)20.8(–25.0) μm in polar axis, (22.5–) 25.4(–28.8) μm in equatorial diameter; P/E = (0.70–)0.82(–0.95), oblate to oblate spheroidal in shape, circular to rhomboidal in equatorial view, semiangular in polar view. Colpi 0.55–0.65 times the length of polar axis, 17.6–21.5 × 3.8–5.8 μm, narrowing to rounded ends toward the pole with large apocolpium and narrowing to pointed ends towards the pole with small apocolpium,



Figs. 105–112. SEM micrographs of pollen of *Flemingia macrophylla* var. *philippinensis* (105–108) and *F. strobilifera* (109–112). 105, 109: Polar view. 106, 110: Equatorial view showing aperture. 107, 111: Equatorial view showing mesocolpium. 108, 112: Enlargement of mesocolpium. Scales = 10 µm (105–107, 109–111), 1 µm (108, 112).



Figs. 113–120. SEM micrographs of pollen of *Rhynchosia acuminatifolia* (113–116) and *R. minima* (117–120). 113, 117: Polar view. 114, 118: Equatorial view showing aperture. 115, 119: Equatorial view showing mesocolpium. 116, 120: Enlargement of mesocolpium. Scales = 10 μm (113–115, 117–119), 1 μm (116, 120).



Figs. 121–124. SEM micrographs of pollen of *Rhynchosia volubilis* (121–124). 121: Polar view. 122: Equatorial view showing aperture. 123: Equatorial view showing mesocolpium. 124: Enlargement of mesocolpium. Scales = 10 μm (121–123), 1 μm (124).

colpus membrane ±smooth, margins with a almost complete and partly rugulate tectum; endoaperture circular to lalongate, 5–5.9 × 5.8–9.2 μm. Sexine semitectate; mesocolpium reticulate; muri 0.4–0.9 μm wide; lumina 0.4–2.6 μm in diameter, rugulate to granulate.

Keys to the genera and species

Key to the genera of the Japanese Phaseoleae and keys to the species of the genera including plural species are provided separately. The latter genera are shown with an asterisk in the first key.

(1) **Key to the genera**:

1. Pollen 6-porate having each one pair of apertures on each of the angles; peroblate to oblate in shape, depressed oval in equatorial view .... *Dumasia*
1. Pollen 3-porate or 3-colporate 2
2. Pollen 3-porate 3
2. Pollen 3-colporate 4
3. Pollen grains elliptical in equatorial view .... *Vigna** excluding *V. adenantha*
3. Pollen grains circular to rhomboidal in equatorial view .... *Erythrina variegata*
4. Pollen heteropolar 5
4. Pollen isopolar 6
5. Sculpture perforate with ±rugulate sculpture on the surface .... *Canavalia**
5. Sculpture reticulate .... *Rhynchosia**
6. Pollen more than 45 μm in polar axis .... *Mucuna**

6. Pollen less than 40 μm in polar axis 7
7. Colpi less than 0.6 times the length of polar axis [colpus membrane granulate to verrucate] 8
7. Colpi more than 0.6 times the length of polar axis 10
8. Endoapertures10.8–15 × 6.6–10.9 μm in size, lolongate; mesocolpium granulate, microreticulate or perforate .... *Apios*
8. Endoapertures less than 9 μm in size, circular to lolongate 9
9. Endoaperture circular, 5.8–6.7 μm in diameter; mesocolpium reticulate .... *Dunbaria*
9. Endoaperture circular to lolongate, 5–8.4 × 3.3–6.3 μm in size; mesocolpium granulate to rugulate .... *Amphicarpaea*
10. P/E less than 1.00 11
10. P/E more than 1.00 12
11. Endoaperture lolongate to circular, 4.1–7.5 μm long, 3.3–5.9 μm wide; sculpture reticulate with lumina 0.25–2.5 μm in size .... *Flemingia**
11. Endoaperture circular, 4.0–6.6 μm across; sculpture reticulate with lumina 3.0–7.0 μm in size .... *Vigna adenantha*
12. Endoaperture more than 5.5 μm long (when lalongate) or in diameter 13
12. Endoaperture less than 5.5 μm in size 14
13. Colpi narrowing to pointed ends .... *Galactia*
13. Colpi narrowing slightly to pointed ends .... *Pueraria**
14. Pollen grains 17.5–27.5 μm in polar axis, 16.3–25.0 μm in equatorial diameter .... *Glycine**
14. Pollen grains 25.0–35.0 μm in polar axis, 23.8–32.5 μm in equatorial diameter .... *Cajanus*

(2) **Keys to the species**:

(3)–(6) *Mucuna*

1. Colpi slightly narrowing to rounded ends .... *M. macrocarpa*
1. Colpi narrowing to pointed ends 2
2. Sculpture of mesocolpium perforate; colpus margins with perforate to microreticulate sculpture ...... *M. gigantea*
2. Sculpture of mesocolpium reticulate 3
3. Colpus membrane granulate to verrucate; lumina 1.0–3.0 μm in diameter .... *M. membranacea*
3. Colpus membrane verrucate; lumina 0.8–1.8 μm in diameter .... *M. sempervirens*

(7)–(9) *Canavalia*

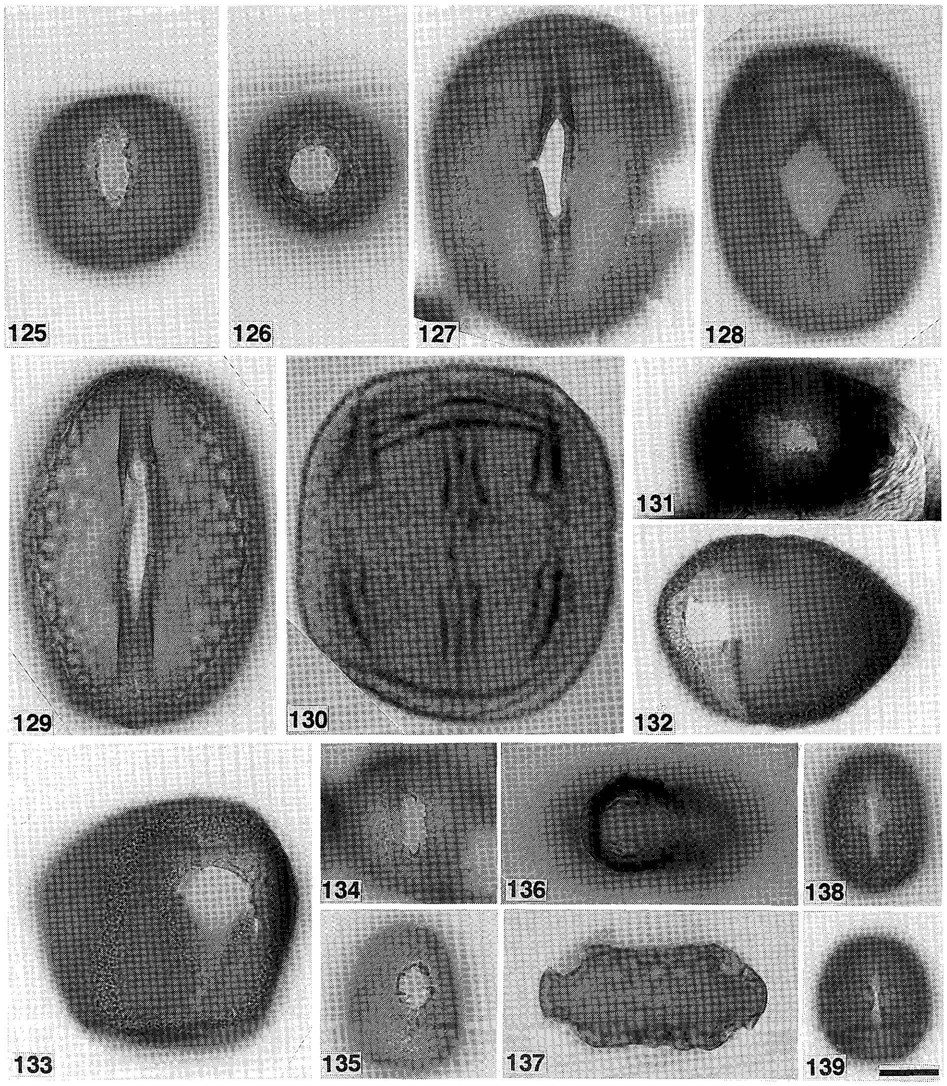
1. Apocolpia same between two poles, verrucate-perforate and granulate .... *C. cathartica*
1. Apocolpia different in sculpture between two poles, verrucate to perforate to granulate in one and granulate in the other ... 2
2. Pollen grains 30–34 μm in polar axis, 40.0–47.5 μm in equatorial diameter, P/E = ca. 0.58; colpi fusing to each other at the pole .... *C. lineata*
2. Pollen grains 35.0–43.8 μm in polar axis, 47.5–58.8 μm in equatorial diameter, P/E = (0.65–)0.75(–0.81); colpi separated each other at the pole .... *C. rosea*

(13)–(15) *Glycine*

1. Sculpture perforate–rugulate or psilate .... *G. koidzumii*
1. Sculpture reticulate–rugulate 2
2. Colpus membrane ±smooth or ±granulate, margins undifferentiated from mesocolpium .... *G. tabacina*
2. Colpus membrane granulate, margin with a complete smooth tectum .... *G. max* (subsp. *soja*)

(16)–(17) *Pueraria*

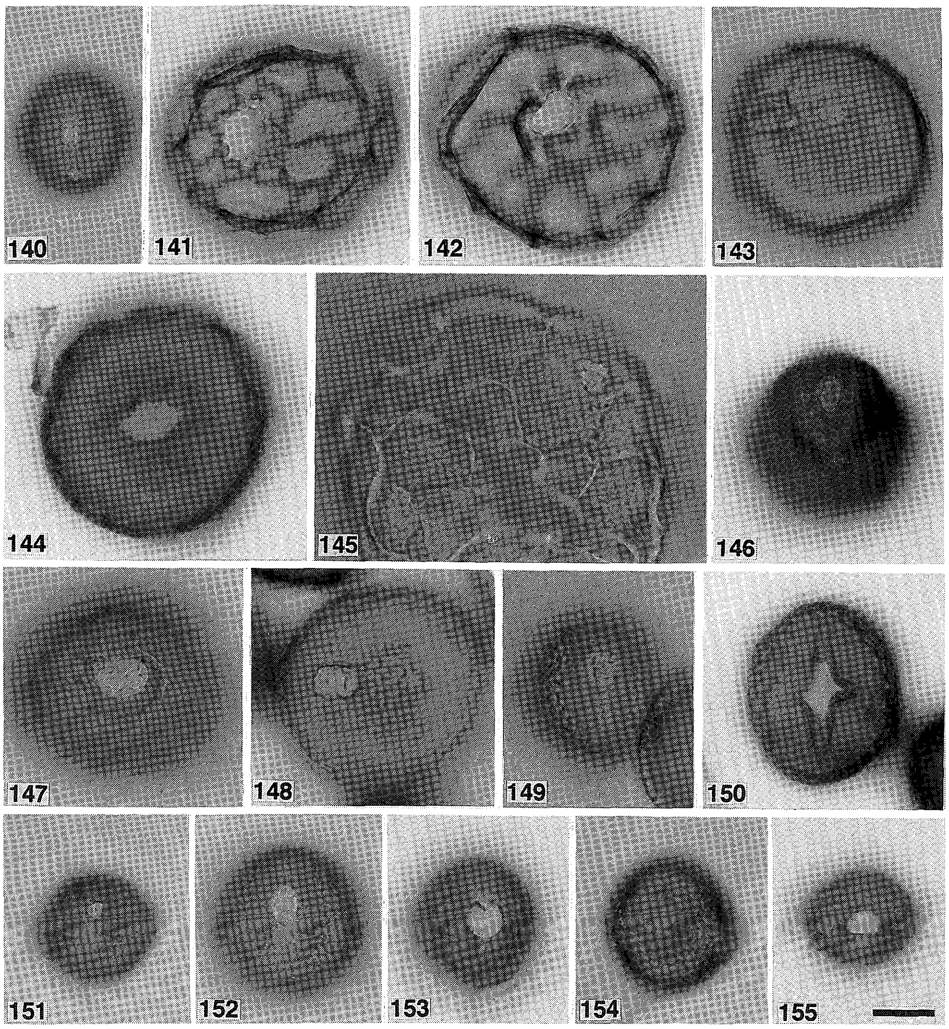
1. Colpi 14–16 μm long; mesocolpium reticulate; lumina 0.8–1.7 μm in diameter, with granules .... *P. lobata*
1. Colpi 16.2–17.5 μm long; mesocolpium reticulate to perforate; lumina 0.1–0.8 μm in diameter .... *P. montana*



Figs. 125–139. LM micrographs showing apertures. 125. *Apios fortunei*. 126. *Erythrina variegata*. 127. *Mucuna gigantea*. 128. *M. macrocarpa*. 129. *M. membranacea*. 130. *M. sempervirens*. 131. *Canavalia cathartica*. 132. *C. lineata*. 133. *C. rosea*. 134. *Galactia tashiroi*. 135. *Amphicarpaea bracteata* subsp. *edgeworthii*. 136, 137. *Dumasia truncata*. 138. *Pueraria lobata*. 139. *P. montana*. Scale = 10 μm.

(18)–(25) *Vigna*

1. Pollen grains 3-colporate ... *V. adenantha*
1. Pollen grains 3-porate, rarely 4-porate 2
2. Pollen grains (40.0–)54.8(–72.5) μm in polar axis, (45.0–)62.7(–87.5) μm in equatorial diameter .... *V. vexillata* (var. *vexillata*)
2. Pollen grains less than 40.0(–45) μm long, 45.0(–55.0) μm in equatorial diameter 3
3. Sculpture within lumina verrucate to



Figs. 140–155. LM micrographs showing apertures. 140. *Glycine max* subsp. *soja*. 141. *Vigna angularis* var. *nipponensis*. 142. *V. minima* var. *minor*. 143. *V. minima* var. *minima*. 144. *V. reflexopilosa*. 145. *V. vexillata* var. *vexillata*. 146. *V. adenantha*. 147. *V. luteola*. 148. *V. marina*. 149. *Cajanus scarabaeoides*. 150. *Dunbaria villosa*. 151. *Flemingia macrophylla* var. *philippinensis*. 152. *F. strobilifera*. 153. *Rhynchosia acuminatifolia*. 154. *R. minima*. 155. *R. volubilis*. Scale = 10 μm.

rugulate 4

3. Sculpture within lumina perforate to verrucate 5

4. Pollen grains generally larger than below: (27.5–)37.1(–42.5) μm in polar axis, (32.5–)41.5(–52.5) μm in equatorial diameter; lumina 2.5–10.5 μm in diameter; sculpture within lumina verrucate to rugulate .... *V. reflexopilosa*

4. Pollen grains generally smaller than above: (27.5–)30.3(–35.0) μm in polar axis, (27.5–)34.8(–42.5) μm in equatorial diameter; lumina 0.9–2.1 μm in diameter; sculpture within lumina verrucate ....

.... *V. marina*

5. Polar view mostly semiangular, sometimes circular; pores less than 8.0 μm in diameter; maximum lumina less than 8.0 μm in diameter .... *V. luteola*
5. Polar view semiangular to circular; pores less than 8.0 μm in diameter; maximum lumina more than 8.0 μm in diameter ... 6
6. Muri more than 0.4 μm wide .... *V. angularis* (var. *nipponensis*)
6. Muri ca. 0.3 μm wide .... 7 *V. minima*
7. Pollen grains (22.5–)25.7(–30.0) μm in polar axis, (27.5–)29.8(–32.5) μm in equatorial diameter .... var. *minima*
7. Pollen grains more than 27.5 μm in polar and equatorial axis .... var. *minor*

(28)–(29) *Flemingia*

1. Pollen grains smaller, (17.5–)20.7(–23.8) μm in polar axis, 18.8–25.0 μm in equatorial diameter; colpi 11.6–15 × 2.5–4.2 μm in size .... *F. macrophylla* (var. *philippinensis*)
1. Pollen grains larger, (22.5–)26.6(–30.0) μm in polar axis, 22.5–30.0 μm in equatorial diameter; colpi 14.6–18.6 × 4.2–8 μm in size .... *F. strobilifera*

(30)–(32) *Rhynchosia*

1. Pollen grains slightly heteropolar; colpi narrowing to pointed ends ...... *R. minima*
1. Pollen grains distinctly heteropolar; colpi narrowing to a rounded end and a pointed end 2
2. Colpi 17.6–21.5 μm long, lumina 0.4–2.6 μm in diameter .... *R. volubilis*
2. Colpi 12–13.5 μm long, lumina 0.4–0.8 μm in diameter .... *R. acuminatifolia*

Discussion

Pollen morphology of the Phaseoleae was characterized by Ferguson and Skvarla (1981) by whom it was generally regarded as specialized, particularly in the very thick endexine and almost complete loss of a foot layer. The Japanese species of the tribe show diversifications in pollen types (3-colporate, 3(–4)-porate, and 6-porate), polarity (heteropolar or isopolar), pollen size, germinal apertures and sculpture patterns. The data based on our observations using SEM and LM are summarized in Table 2. Among the Japanese Phaseoleae *Dumasia truncata* has a unique pollen grain which was described and illustrated Ikuse (1954) for the first time. The pollen is 6-porate having one pair of apertures on each of the angles, triangular or very rarely quadrangular in polar view, and flattened with a very short polar axis in equatorial view.

1. *Amphicarpaea*

Pollen of *Amphicarpaea* has been recorded as tricolporate, triporate or 4–5-porate (Ohashi 1999). The first type was reported for *A. africana* (Hook. f.) Harms by Meeson (1974). However, pollen of *A. bracteata* (L.) Fernald subsp. *edgeworthii* (Benth.) H. Ohashi (or *A. edgeworthii* Benth., or *A. edgeworthii* Benth. var. *japonica* Oliver) is described as tricolporate by Ikuse (1956) from Japan, Huang (1972) from Taiwan and Guo et al. (2003) from China; or 3-porate by Huang (1968) and by Meeson (1974). And also, 4–5-porate for *A. bracteata* (L.) Fernald by Meeson (1974) from North America and for *A. bracteata* subsp. *edgeworthii* (as *A. trisperma* Baker) by Liu (1991) from China. Pollen grains of *A. bracteata* subsp. *edgeworthii* is characteristic in having short colpi which are often indistinguishable from the tectum (Fig. 156, A–C). This is true also for *A. bracteata* (Fig. 156, D–F). On the other hand, pollen of *A. africana* (Hook. f.) Harms is distinctly 3-colporate (Meeson 1974 and Fig. 157 in this paper). From these facts the pollen of *Amphicarpaea* is recognized as colporate grains.

Amphicarpaea bracteata and *A. edgeworthii* are regarded as conspecific under, *A. bracteata* (L.) Fernald subsp. *edgeworthii* (Benth.) H. Ohashi. Macro-

Table 2. Pollen data of Japanese Phaseoleae

Taxon	Pollen type	Polar axis (P) (μm)	Equatorial diameter (E) (μm)	P/E
Subtribe **Erythrinae**				
Apios fortunei	tricolporate	(27.0–)31.4(–40.0)	(27.5–)32.0(–35.0)	(0.81–)0.98(–1.09)
Erythrina variegata	tiporate	(27.5–)30.4(–32.5)	(32.5–)33.5(–35.0)	(0.80–)0.91(–1.00)
Mucuna gigantea	tricolporate	(50.0–)55.4(–60.0)	(45.0–)49.4(–57.5)	(1.00–)1.13(–1.28)
M. macrocarpa	tricolporate	(45.0–)47.8(–52.5)	(30.0–)32.9(–37.5)	(1.20–)1.46(–1.75)
M. membranacea	tricolporate	(45.0–)58.8(–65.0)	(37.5–)48.5(–57.5)	(1.00–)1.21(–1.39)
M. sempervirens	tricolporate	ca. 53	ca. 44	ca. 1.2
Subtribe **Diocleinae**				
Canavalia cathartica	tricolporate, heteropolar	(30.6–)32.2(–34.2)	(41.4–)46.9(–52.2)	(0.61–)0.69(–0.80)
C. lineata	tricolporate, heteropolar	30–34	(40.0–)43.4(–47.5)	ca. 0.58
C. rosea	tricolporate, heteropolar	(35.0–)40.1(–43.8)	(47.5–)53.8(–58.8)	(0.65–)0.75(–0.81)
Galactia tashiroi	tricolporate	(22.5–)25.3(–27.5)	(20.0–)21.3(–25.0)	(1.00–)1.19(–1.38)
Subtribe **Glycininae**				
Amphicarpaea bracteata subsp. *edgeworthii*	tricolporate	(25.2–)26.9(–30.6)	(19.8–)21.2(–30.6)	(0.94–)1.28(–1.45)
Dumasia truncata	hexaporate	16–25	(32.5–)34.7(–40.0)	0.43–0.65
Glycine koidzumii	tri- or tetra-colporate	unclear	ca. 15–18	unclear
G. max subsp. *soja*	tricolporate	(17.5–)21.6(–27.5)	(16.3–)19.4(–25.0)	(1.00–)1.12(–1.38)
G. tabacina	tricolporate	21–23	21–23	ca. 1.0
Pueraria lobata	tricolporate	(21.6–)25.7(–29.7)	(18.0–)20.6(–23.4)	(1.08–)1.25(–1.36)
P. montana	tricolporate	(21.6–)23.0(–25.2)	(18.0–)19.7(–21.6)	(1.08–)1.17(–1.30)
Subtribe **Phaseolinae**				
Vigna adenantha	tricolporate	(20.0–)22.4(–25.0)	(30.0–)31.5(–35.0)	(0.64–)0.71(–0.83)
V. angularis var. *nipponensis*	triporate	(27.5–)33.4(–37.5)	(32.5–)36.5(–42.5)	0.85(–0.92)(1.00–)
V. luteola	triporate	(32.5–)34.9(–37.5)	(37.5–)39.3(–42.5)	(0.81–)0.89(–0.94)
V. marina	triporate	(27.5–)30.3(–35.0)	(27.5–)34.8(–42.5)	(0.81–)0.89(–0.95)
V. minima				
var. *minina*	triporate	(22.5–)25.7(–30.0)	(27.5–)29.8(–32.5)	(0.69–)0.86(–1.00)
var. *minor*	triporate	(32.5–)35.7(–40.0)	(37.5–)38.7(–42.5)	(0.85–)0.92(–1.00)
V. reflexopilosa	tri (–tetra)porate	(27.5–)37.1(–42.5)	(32.5–)41.5(–52.5)	(0.73–)0.89(–1.00)
V. vexillata var. *vexillata*	triporate	(40.0–)54.8(–72.5)	(45.0–)62.7(–87.5)	(0.80–)0.88(–1.00)
Subtribe **Cajaninae**				
Cajanus scarabaeoides	tricolporate	(25.0–)28.4(–35.0)	(23.8–)26.8(–32.5)	(0.91–)1.06(–1.20)
Dunbaria villosa	tricolporate	(25.0–)29.9(–37.5)	(25.0–)29.4(–35.0)	(0.92–)1.02(–1.18)
Flemingia macrophylla var. *philippinensis*	tricolporate	(17.5–)20.7(–23.8)	(18.8–)21.2(–25.0)	(0.88–)0.98(–1.13)
F. strobilifera	tricolporate	(22.5–)26.6(–30.0)	(22.5–)27.2(–30.0)	(0.82–)0.98(–1.10)
Rhynchosia acuminatifolia	tricolporate, heteropolar	(19.8–)24.9(–27.0)	(21.6–)25.8(–28.8)	(0.92–)0.97(–1.00)
R. minima	tricolporate	(21.6–)23.0(–25.2)	(21.6–)22.9(–27.0)	(0.87–)1.01(–1.08)
R. volubilis	tricolporate, heteropolar	(17.5–)20.8(–25.0)	(22.5–)25.4(–28.8)	(0.70–)0.82(–0.95)

(diam.): diameter

Shape class	Colpus (μm)	Endoaperture		Pore	
		shape	size (μm)	shape	size (μm)
suboblate–prolate spheroidal	15.8–22.5 × 3.3–8.0	lalongate	10.8–15 × 6.6–10.9		
suboblate–oblate spheroidal				lalongate–circular–lolongate	6.25–10.8 × 5.8–9.2
prolate spheroidal–subprolate	41.6–47.5 × 2–4	lolongate	13.3–17.1 × 3.3–5		
subprolat–prolate	33.3–37.5 × 2–4.2	lolongate	10.8–15 × 3.3–4.2		
prolate spheroidal–prolate	47.5–52.5 × 2.5–3.3	lolongate	15–20.8 × 4.1–5		
subprolate	ca. 3.2 × 2	lolongate	ca. 15 × 4		
oblate–suboblate	25–29.2 × 3–7	lalongate	9.1–12.5 × 14–17.5		
oblate	25 × 3.3–8	lalongate	4.1–5.9 × 11.6–14.2		
oblate–suboblate	29–34 × 4.1–6.7	lalongate	ca. 8 × 12		
prolate spheroidal–prolate	18.3–19.2 × 2–5	lolongate	5.8–7.5 × 3–7		
oblate spheroidal–prolate	ca. 14.5 × 3	lolongate–circular	5–8.4 × 3.3–6.3		
peroblate–oblate				angular–circular–lalongate	2.5–6 × 6–9
unclear	variable	circular	ca. 3 (diam.)		
prolate spheroidal–prolate	12.5–16.7 × 1.6–3.8	circular–subcircular	3.3–5 × 3.3–4.6		
spheroidal–prolate spheroidal	14.4–17.5 × 3.9–5.5	circular	ca. 5.5 (diam.)		
prolate spheroidal–prolate	14–16 × 1.6–3.3	circular–lolongate	7.5–8.3 × 7.5–8.3		
prolate spheroidal–subprolate	16.2–17.5 × 1.4–2.3	circular–lolongate	5–8.3 × 3.3–5.9		
oblate–suboblate	16.6 × 8–10.8	circular	4–6.6 (diam.)		
suboblate–oblate spheroidal				lalongate–circular–lolongate	5–8.3 (diam.)
suboblate–oblate spheroidal				lolongate	7.5–9.1 × 5–6.6
suboblate–oblate spheroidal				circular	5.0–7.5 (diam.)
oblate–oblate spheroidal				lalongate–circular–lolongate	4.2–5.5 (diam.)
suboblate–oblate spheroidal				lalongate–circular–lolongate	5.4–9.2 (diam.)
oblate–oblate spheroidal				lalongate–circular–lolongate	5.8–10 (diam.)
suboblate–oblate spheroidal				circular	7.5–15 (diam.)
oblate spheroidal–subprolate	19–20.5 × 2.3–3.6	lalongate–circular	4–5 × 3.3–5		
oblate spheroidal–subprolate	12.5–15 × 2.9–4.5	circular	5.8–6.7 (diam.)		
suboblate–prolate spheroidal	11.6–15 × 2.5–4.2	lolongate–circular	4.1–5.9 × 3.3–4.6		
suboblate–prolate spheroidal	14.6–18.6 × 4.2–8	circular–lolongate	5–7.5 × 3.3–5.9		
oblate spheroidal	12–13.5 × 3.5–5.5	lalongate–circular–lolongate	5.8–7.5 × 5.8–9.2		
suboblate–prolate spheroidal	15–22.5 × 3.3–5	lalongate–circular–lolongate	4.1–6.6 × 5–8.3		
oblate–oblate spheroidal	17.6–21.5 × 3.8–5.8	circular–lalongate	5–5.9 × 5.8–9.2		

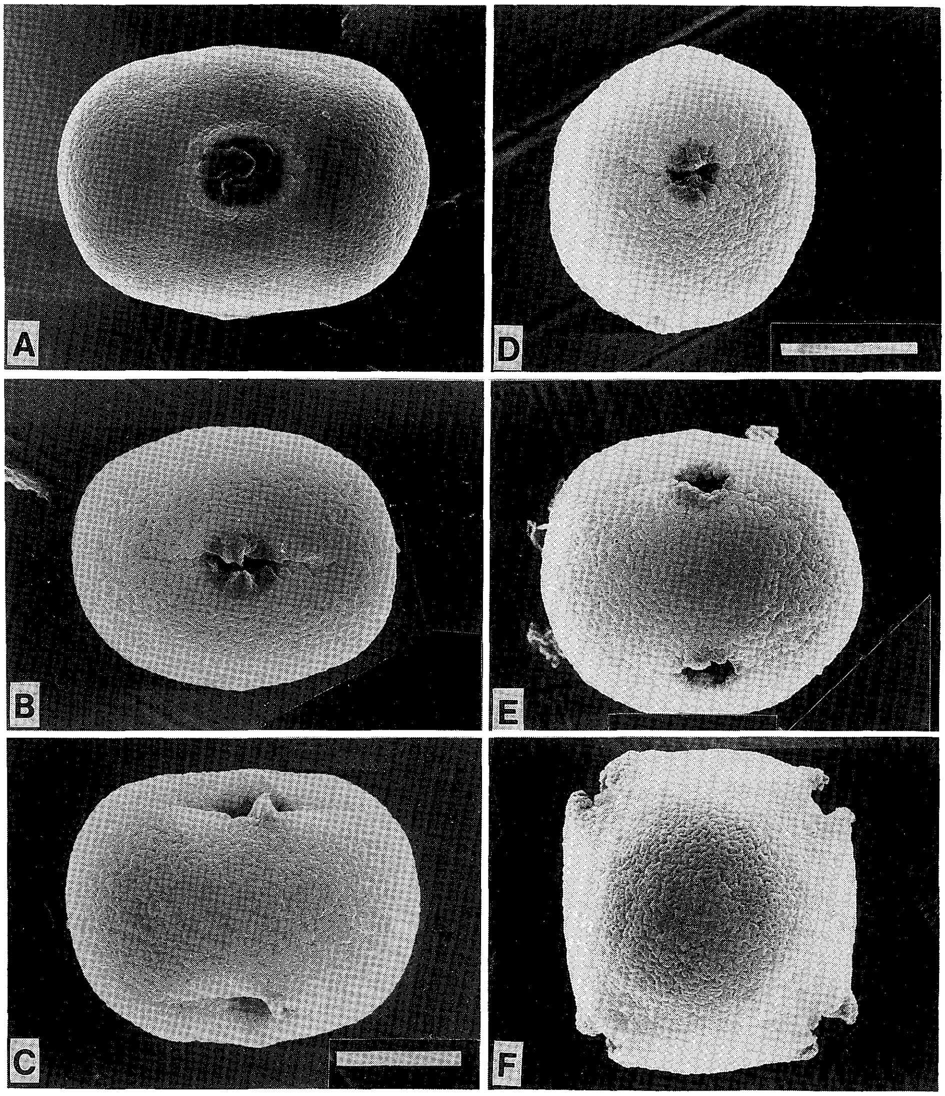


Fig. 156. Pollen of *Amphicarpaea bracteata* subsp. *edgeworthii* (A–C) and subsp. *bracteata* (D–F). showing variation of colpi. A: Scarcely developed colpus (voucher : Japan, Shiga Pref., Ohashi & al. 9328, TUS). B–C: Well developed colpus (voucher: Japan, Miyagi Pref., Kimura & Sugaya s.n., 9 Sept. 1953, TUS). D–F: *Amphicarpaea bracteata* subsp. *bracteata* (voucher: USA, Barrell 32a-58, A), showing narrow but distinct colpi. A–E: equetrial view, F: polar view. Scale = 10 μm.

mophological differences between these species are limited only to the shape of bracts and calyx-lobes (Turner and Fearing 1965, Ohashi 1966, 2001). However, Lee and Hymowicz (2001) considered that *A. bracteata* and *A. edgeworthii* are separate species based on their analyses of chloroplast DNA in the subtribe Glycininae (Phaseoleae). These species are palynologically distinct from each other. *Amphicarpaea*

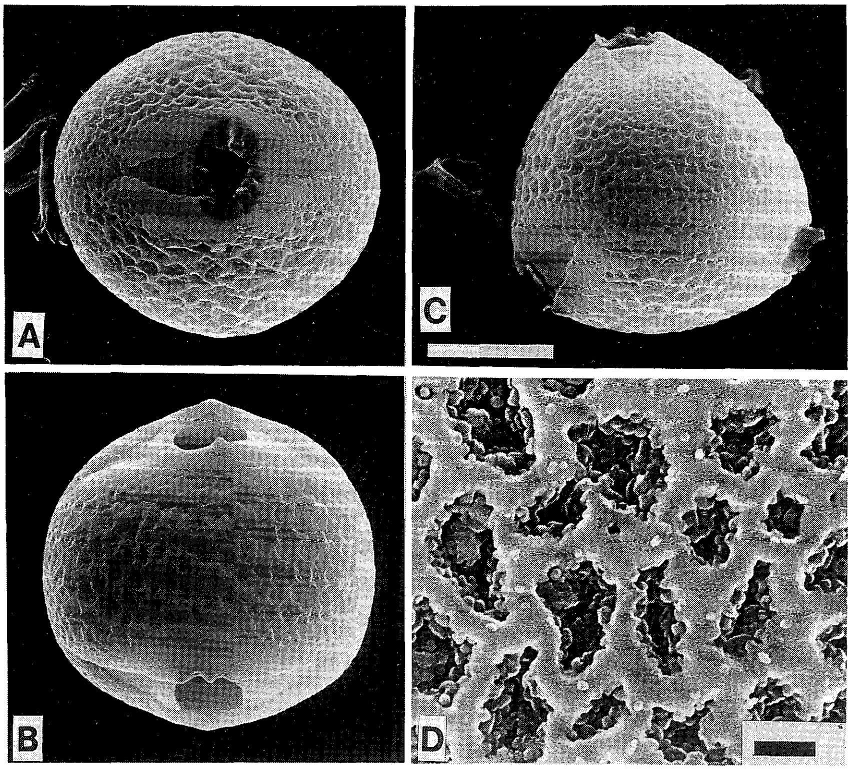


Fig. 157. Pollen of *Amphicarpaea africana* (voucher: Congo., T.K. 3088, E) showing distinct 3-colporate pollen grain. A–B: Equetrial view, C: polar view, D: sculpture on mesocolpium. Scales = 10 μm (A–C), 1 μm (D).

bracteata has 3-colporate pollen grains, while *A. edgeworthii* 4- or sometimes 5-colporate ones. They are here kept at the subspecific rank on the basis of the macromorphological and geographical evidence. The differences between these taxa are summarized in the following key:

1. Bracts ovate to broadly ovate, apex acute; lowest calyx-lobes narrowly triangular to triangular, 2–3 μm long. Pollen 3-colporate. Distributed in Asia: Nepal, India, Indo-China, China, Taiwan, Korea, Japan, and Russia: Far East. .... *A. bracteata* subsp. *edgeworthii*
1. Bracts obovate to broadly obovate, apex obtuse; lowest calyx-lobes triangular, 1–2 μm long. Pollen 4 (–5)-colporate. Distributed in N. America .... *A. bracteata* subsp. *bracteata*

Turner and Fearing (1964) considered that *Amphicarpaea africana* is more distinct from *A. edgewortii* and *A. bracteata.* This view supports a supposition of Meeson (1974) that the pollen of the latter two appear to be modifications of the basic form of *A. africana* by loss of the colpi and reticulated sexine and an increase or retention in the number of pores.

It needs to reconsider the taxonomic position and relation between these species after comparing all the taxa of the genus by their DNA analyses as well as fossil data. The taxa in *Amphicarpaea* seem to be a good example for studying differentiation and phylogeny of advanced legumes. They are only five comprising four species and one subspecies but disjunctively distributed in Africa, Asia, and North America.

2. *Vigna*

Vigna adenantha has the only tricolporate and verrucate pollen grains among the Japanese species. Floral and pollen characters of the species agree with *Phaseolus*, however, Maréchal et al. (1978) showed the taxonomic position of the species including pollen characters. The species is the only representative of the sect. Leptospron included in subgen. Sigmoidotropis of genus *Vigna*. They did not consider the section as intermediate between genus *Phaseolus* and genus *Vigna*. Further investigation may need to clarify its taxonomic position.

Vigna adenantha is distributed widely in tropical and subtropical regions of the world. Distribution of this species in the Ryukyus and Taiwan was analysed by Tateishi (1988) based on a comparison of seed structure with other Japanese *Vigna*.

We should like to acknowledge pollen samples from herbarium specimens of A and E studied by Ms. J. Iketsu and URO. Thanks to Ms. Iketsu of Adachi High School in Fukushima Prefecture for data and photos of *Amphicarpaea*, Dr. Y. Tateishi of University of the Ryukyus and Mr. I. Kawakami of Irabu High School in Okinawa Prefecture for providing specimens of *Glycine koidzumii* and *G. tabacina*, Dr. Y. Kadota of National Science Museum, Tokyo, and Dr. X. Y. Zhu of Botany Institute, Academia Sinica, Beijing, for providing references.

References

Bronkers F. and De Keyser B. 1966. Contribution à l'étude palynologique des Papilionaceae–Phaseoleae–Phaseolinae. I. Observations sur quatre espèces de *Dolichos* L. et sur *Lablab niger* Medic. Bull. Jard. Bot. État. Brux. **36**: 57–63.

Bruneau A., Doyle J. J. and Doyle J. L. 1995. Phylogenetic relationships in Phaseoleae: evidence from chloroplast DNA. *In*: Crisp M. D. and Doyle J. J. (eds.): Advances in Legume Systematics. Part 7. Phylogeny. pp. 309–330. Royal Botanic Gardens, Kew.

Doyle J. J., Chappili J. A., Bailey C. D. and Kajita T. 2000. Towards a comprehensive phylogeny of Legumes: Evidence from *rbc*L sequences and non-molecular data. *In*: Herendeen P. S. and Bruneau A. (eds.), Advances in Legume Systematics. Part 9. pp. 1–20. Royal Botanic Gardens, Kew.

Erdtman G. 1960. The acetolysis method. A revised description. Sven. Bot. Tidskr. **54**: 561–564.

—— 1966. Pollen Morphology and Plant Taxonomy. Angiosperms. 553 pp. Almquist & Wiksell, Stockholm. Offset edition with addendum: Hafner, New York.

—— 1969. Handbook of Palynology. 486 pp. Munksgaard, Copenhagen.

Fægri K. and Iversen J. 1989. *In*: Fægri K., Kaland P. E. and Krzywinski K. (eds.), Textbook of Pollen Analysis. 4th ed. 328 pp. John Wiley & Sons, Chichester.

Ferguson I. K. 1984. Pollen morphology and biosystematics of the subfamily Papilionoideae (Leguminosae). *In*: Grant W. F. (ed.), Plant Biosystematics. pp. 377–394. Academic Press Canada, Toronto.

Ferguson I. K. and Skvarla J. J. 1981. The pollen morphology of the subfamily Papilionoideae (Leguminosae). *In*: Polhill R. M. and Raven P. H. (eds.), Advances in Legume Systematics. pp. 859–896. Royal Botanic Gardens, Kew.

Guo X. M., Qiao Y. K., Wang Y. X. Liu Y. J. and Liu J. Z. 2003. Observation on pollen and leaf epidermis of *Amphicarpaea edgeworthii* by SEM. Acta Bot. Boreal.-Occident. Sin. **23**: 2072–2076.

Horvat F. and Stainier F. 1980. L'Étude de l'exine dans le complexe *Phaseolus-Vigna* et dans des genres apparentés. IV. Pollen et Spores **22**: 139–172.

Huang T. C. 1968. Pollen grains of Formosan plants (4). Leguminosae. Taiwania (14): 154–196.

—— 1972. Pollen Flora of Taiwan. National Taiwan University Botany Department Press, Taipei.

Iketsu J. 1988. A taxonomic study on *Amphicarpaea* (Leguminosae). Unpublished thesis for Master of Science, Tohoku University, Sendai.

Ikuse M. 1954. Pollen grains of Leguminosae obtained in Japan, especially of their unusual forms. J. Jpn. Bot. **29**: 1–10, plate 4 (in Japanese).

—— 1956. Pollen Grains of Japan. Hirokawa

Publishig Co., Tokyo (in Japanese).

Kajita T., Ohashi H., Tateishi Y., Bailey C. D. and Doyle J. J. 2001. *rbcL* and legume phylogeny, with particular reference to Phaseoleae, Millettieae, and Allies. Syst. Bot. **26**: 515–536.

Lackey J. A. 1977. A revised classification of the tribe Phaseoleae (Leguminosae: Papilionoideae), and its relation to canavanine distribution. Bot. J. Linn. Soc. **74**: 163–178.

—— 1981. Tribe 10. Phaseoleae DC. (1825). *In*: Polhill R. M. and Raven P. H. (eds.), Advances in Legume Systematics. Part **1**: 301–327. Royal Botanic Gardens, Kew.

Lee J. and Hymowitz T. 2001. A molecular phylogenetic study of the subtribe Glycininae (Leguminosae) derived from the chloroplast DNA *RPS*16 intron sequences. Amer. J. Bot. **88**: 2064–2073.

Liu B. 1991. Pollen morphology of Phaseoleae in China and its significance to the art. Bot. Research (Inst. Bot. Acad. Sinica) (5): 59–86, pls. 1–34.

Makino H. 1978. Palynological studies in Leguminosae (Lotoideae) tribe Phaseoleae. Hoehnea **7**: 47–98.

Maréchal R. and Baudet J.C. 1977. Transfert du genre africain *Kerstingiella* Harms à *Macrotyloma* (Wight & Arn.) Verdc. (Papilionaceae). Bull. Jard. Bot. Nat. Belg. **47**: 49–52.

——, Mascherpa J.-M. and Stainier F. 1978. Étude taxonomique d'un groupe complexe d'espèces des genres *Phaseolus* et *Vigna* (Papilionaceae) sur la base de données morphologiques et polliniques, traitées par l'analyse informatique. Boissiera **28**: 1–273.

Meeson B. W. 1974. Pollen morphology of *Amphicarpaea* (Leguminosae: Phaseoleae). Sida **5**: 338–340.

Nakamura J. 1980. Diagnostic characters of pollen grains of Japan. Special Publications from the Osaka Museum of Natural History **12**: pls. 1–157, **13**: 1–91.

Ohashi H. 1966. Leguminosae. *In*: Hara H. (ed.), Flora of Eastern Himalaya. pp. 135–166. University Tokyo Press, Tokyo.

—— 1971. A taxonomic study of the tribe Coronilleae (Leguminosae), with a special reference to pollen morphology. J. Fac. Sci., Univ. Tokyo, Sect. III (Botany) **11**: 25–92.

—— 1999. The genera, tribes and subfamilies of Japanese Leguminosae. Sci. Rep. Tohoku Univ. 4th ser. (Biol.) **40**: 186–269.

—— 2001. Leguminosae. *In*: Iwatsuki K., Ohba H. and Boufford D. E. (eds.), Flora of Japan **2b**: 213–279. Kodansha Ltd., Tokyo.

—— and Takahashi H. 1981. Pollen morphology of *Vigna angularis* (Leguminosae). Bot. Mag. Tokyo **94**: 177–180.

Polhill R. M. 1994. Synopsis of legume genera. *In*: ILDIS and CHCD, Phytochemical Dictionary of the Leguminosae. **1**: pp. xlix-lvii. Chapman & Hill, London.

Punt W., Blackmore S., Nilsson S. and Thomas A. Le 1994. Glossary of Pollen and Spore Terminology. Laboratory of Palaeobotany and Palynology, LPP Contributions Series, No. **1**, 71 pp. LPP Foundation, Utrecht.

Shimakura M. 1973. Palynomorphs of Japanese plants. Special Publications from the Osaka Museum of Natural History **5**: 1–60, pls. 1–122.

Stainier F. 1974. Contribution à l'étude palynologique des Papilionaceae–Phaseolae–Phaseolinae. III–Étude de quelques espèces des genres *Phaseolus* L., *Vigna* Savi et *Physostigma* Balf. Bull. Jard. Bot. Natl. Belgique **44**: 1–15.

—— 1976. Note sur le pollen de quelques espèces sud-américaines du complexe *Phaseolus-Vigna*. Pollen et Spores **18**: 523–531.

—— and Horvat F. 1978. L'étude de l'exine du pollen dans le complexe *Phaseolus-Vigna* et dans des genres apparentés. I. Pollen et Spores **22**: 195–214.

—— and —— 1979. L'étude de l'exine du pollen dans le complexe *Phaseolus-Vigna* et dans des genres apparentés. III. Pollen et Spores **21**: 17–30.

Tateishi Y. 1988. Distribution and distribution mechanism of *Vigna adenantha* (Leguminosae) in Taiwan and Ryukyus. J. Jpn. Bot. **63**: 313–318 (in Japanese).

Turner B. L. and Fearing O. S. 1965. A taxonomic study of the genus *Amphicarpaea* (Leguminosae). The Southwestern Naturalist **9**: 207–218.

Verdcourt B. 1970a. Studies in the Leguminosae–Papilionoideae for the 'Flora of Tropical East Africa': III. Kew Bull. **24**: 379–447.

—— 1970b. Studies in the Leguminosae–Papilionoideae for the 'Flora of Tropical East Africa': IV. Kew Bull. **24**: 507–569.

—— 1978. The demise of two geocarpic legume genera. Taxon **27**: 219–222.

—— 1980. The correct name for the Bambara Groundnut. Kew Bull. **35**: 474.

Viviani T., Conte L., Cristofolini G. and Speranza M. 1991. Sero-systematic and taximetric studies on the Phaseoleae (Fabaceae) and related tribes. Bot. J. Linn. Soc. **105**: 113–136.

Wojciechowski M.F. 2003. Reconstructing the phylogeny of legumes (Leguminosae): an early 21st century perspective. *In*: Klitgaard B. B. and Bruneau A. (eds.), Advances in Legume Systematics. **10**.

Higher Level Systematics. pp. 5–35. Royal Botanic Gardens, Kew.

Ye B. and Ohashi H. 2002. Morphology and polymorphism in the pollen of *Christia* and *Uraria* (Leguminosae: Papilionoideae). J. Jpn. Bot. **77**: 150–162.

大橋広好[a]，根本智行[b]，小野寺竜一[c]：日本産マメ科インゲンマメ連の花粉形態

インゲンマメ連はマメ亜科 Papilionoideae の中で最大のグループで形態が多様であり，1977年には89属約1500種を含むと推定されていた（Lackey 1977）．最近では83属とされている（Polhill 1994）．Lackey（1981）はこれを10亜連に分類したが，この分類体系 は花粉形態の特徴に一致しないことが指摘されている（Ferguson and Skvarla 1981）．また，最近の化学分類学や分子系統解析ではインゲンマメ連は多系統であることが示されている（Doyle et al. 2000, Kajita et al. 2001, 他）．本研究は未だ花粉形態の調べられていない多くの種を含む日本産インゲンマメ連について，全種の花粉形態を記録し，それによってインゲンマメ連分類体系の改良と日本の花粉フロラとに役立つためのデータを作ることを目的とした．観察方法として走査型電子顕微鏡と光学顕微鏡とを併用した．インゲンマメ連の花粉は透過型電子顕微鏡（TEM）によって層壁 sporoderm の構造の特徴が明らかにされている（Ferguson and Skvarla 1981）．日本産インゲンマメ連花粉の TEM による調査については今後の研究に待ちたい．

日本にはインゲンマメ連は13属あり，これは世界のインゲンマメ連の13%に当たる（Ohashi 1999）．本論文では日本の全自生種に帰化と思われるデイコ *Erythrina variegata* L.を加えて全体で14属31種1変種（Table 1）の花粉形態を調べた．それらの花粉型 pollen type（= pollen class, pollen group），花粉のサイズと類型 shape class，発芽口 aperture，外表層模様 について記載した（Table 2）．また，全種について花粉の極観 polar view，発芽口を中心とした赤道面，発芽口に挟まれた部分 mesocolpium の外表層の模様を走査型電子顕微鏡による写真（Figs. 1–124）とさらに大部分の種については発芽孔を光学顕微鏡写真とで図示した（Figs. 125–155）．

ヤブマメ属の花粉は溝孔型 colporate type とも孔粒 porate type とも記載されていたが，今回ヤブマメ属は溝孔型であることを示した．アメリカの *Amphicarpaea bracteata* とアジアの *A. edgeworthii* は外部形態では非常によく似ており，同属内の他種との違いと比較すると別種と考えがたく，地理的亜種としてアジアのものは *Amphicarpaea bracteata* subsp. *edgeworthii* とされているが，花粉型が異なっている．ヤブマメ属の種の分類と進化は興味深い問題であると思われる．

（東北大学理学部生物学教室，
[a]現所属：東北大学附属植物園津田記念館，
[b]現所属：石巻専修大学基礎理学科，
[c]現住所：124-[redacted] 東京都葛飾区[redacted]）